This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.

+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.

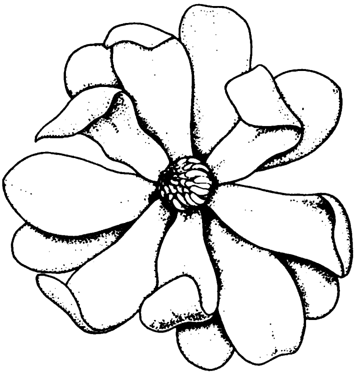
+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.

+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

LIBRARY
OF THE
ARNOLD ARBORETUM
JAMAICA PLAIN



HARVARD UNIVERSITY

*5

mh
126.6
B73

JUNE, 1920 BULLETIN 217

University of Vermont and State Agricultural College

Vermont Agricultural Experiment Station

BURLINGTON, VERMONT

BLACKBERRIES OF NEW ENGLAND—THEIR CLASSIFICATION

By EZRA BRAINERD and A. K. PEITERSEN

A UP 209 5/22/90 #45.00

BURLINGTON
FREE PRESS PRINTING COMPANY
1920

THE BOARD OF CONTROL

THE EXECUTIVE COMMITTEE OF THE BOARD OF TRUSTEES
G. W. BAILEY, Essex Junction.
N. K. CHAFFEE, Rutland.
ROBERT ROBERTS, Burlington.
ELIAS LYMAN, Burlington.
G. M. POWERS, Morrisville.
C. J. WRIGHT, Williston.

THE ADVISORY COUNCIL

HON. ROBERT ROBERTS, Burlington,
HON. N. K. CHAFFEE, Rutland,
Representing the University Board of Trustees.
MR. L. K. OSGOOD, Rutland,
MR. A. C. WELLS, Bakersfield,
Representing State Grange.
HON. C. W. GATES, Franklin,
HON. A. A. DUNKLEE, Vernon,
Representing the Vermont Dairymen's Association.
HON. V. I. SPEAR, Randolph, Representing the Vermont Sugar Makers' Association.
MRS. G. A. DAVIS, Windsor,
MRS. J. B. CHASE, Lyndonville,
Representing the Federation of Women's Clubs.
MR. E. B. CORNWALL, Middlebury, Representing the State Federation of Farm Bureaus.
THE PRESIDENT, DEAN and DIRECTOR, THE DIRECTOR OF THE EXTENSION SERVICE, COMMISSIONER OF EDUCATION and COMMISSIONER OF AGRICULTURE, *Ex-officio*.

THE OFFICERS OF THE STATION

J. L. HILLS, Sc. D., Director.
F. A. RICH, V. S., M. D., Veterinarian.
C. H. JONES, M. Sc., Chemist.
M. B. CUMMINGS, Ph. D., Horticulturist.
B. F. LUTMAN, Ph. D., Plant Pathologist.
G. P. BURNS, Ph. D., Botanist.
H. B. ELLENBERGER, Ph. D., Animal and Dairy Husbandman.
L. H. FLINT, M. Sc., Assistant Botanist.
E. J. DOLE, A. M., Assistant Botanist.
A. H. GILBERT, M. Sc., Associate Plant Pathologist.
J. A. NEWLANDER, B. S., Associate Dairy Husbandman.
G. F. ANDERSON, Assistant Chemist.
W. H. CROCKETT, Editor.
ALEXANDER PARKS, Gardener.
WINIFRED B. KENNEDY, Stenographer.
MAY O. BOYNTON, Ph. B., Librarian.
GUY W. BAILEY, A. B., Treasurer.

☞Copies of the reports and bulletins of the Station are sent free of charge to any address upon application.

☞Address all communications concerning station matters not to individual officers but to the Experiment Station, Burlington, Vt. Address inquiries concerning farm practice to Extension Service, Burlington, Vt.

Director's office, chemical, horticultural and dairy laboratories are in Morrill Hall at the head of Main street; botanical and bacteriological laboratories are at Williams Science Hall, University Place; veterinary laboratories are at 499 Main street. University farm and buildings are on the Williston road, adjoining the University grounds on the east.

BULLETIN 217: BLACKBERRIES OF NEW ENGLAND—THEIR CLASSIFICATION

By Ezra Brainerd and A. K. Peitersen

TABLE OF CONTENTS

I. Present systematic status of Rubus 5
II. The object of this study 5
III. Methods used in determining the systematic rank of a given plant 6
IV. Hybridity among American Rubi 9
V. Hybridity as it affects classification 12
VI. The New England Blackberries 12
Key to the twelve species of New England Rubus § Eubatus 15
Key to some New England hybrids and blend hybrids of Rubus § Eubatus 16
Diagram showing systematic arrangement of New England blackberries 20-21
Illustrations and descriptions of the twelve valid species of Rubus § Eubatus found in New England 22-50
1. *Rubus allegheniensis,* High Bush Blackberry... 23
2. *R. argutus,* Tall Blackberry 27
3. *R. baileyanus,* Bailey's Blackberry............ 49
4. *R. canadensis,* Mountain Blackberry 35
5. *R. elegantulus,* Showy Flowering Blackberry... 37
6. *R. enslenii,* Enslen's Blackberry 47
7. *R. flagellaris,* Whip Blackberry 45
8. *R. frondosus,* Leafy-flowered Blackberry 31
9. *R. hispidus,* Running Swamp Blackberry...... 43
10. *R. pergratus,* Short Blackberry 29
11. *R. setosus,* Bristly Blackberry 41
12. *R. vermontanus,* Vermont Blackberry 39
Illustrations and descriptions of some of New England hybrids and blend hybrids of Rubus § Eubatus......52-79
1. *R. abbrevians* (*R. frondosus* × *setosus*)...... 65
2. *R. andrewsianus* (*R. allegheniensis* × *argutus*). 53
3. *R. arenicola* (*R. baileyanus* × *frondosus*)..... 75
4. *R. elongatus* (*R. allegheniensis* × *flagellaris*).. 71
5. *R. flavinanus* (*R. allegheniensis* × *elegantulus*) 57

6. *R. fraternus* (*R. allegheniensis* × *vermontanus*) 59
7. *R. frondisentis* (*R. pergratus* × *setosus*)..... 63
8. *R. glandicaulis* (*R. allegheniensis* × *setosus*).. 61
9. *R. invisus* (*R. baileyanus* × *flagellaris*)........ 79
10. *R. jacens* (*R. hispidus* × *setosus*) 77
11. *R. jeckylanus* (*R. argutus* × *frondosus*) 55
12. *R. junceus* (*R. canadensis* × *setosus*)......... 67
13. *R. multispinus* (*R. argutus* × *flagellaris*) 73
14. *R. permixtus* (*allegheniensis* × *hispidus*) 69
Additional list of hybrids or suspected hybrids which are found in New England 80-84

I. PRESENT SYSTEMATIC STATUS OF RUBUS

Rubus is one of the most polymorphic genera in the entire plant kingdom. Like Rosa, Hieracium, Crataegus, Salix, and a few other genera it includes many minutely different forms and varieties which are intermediate between the more or less distinct species. This is especially true when one considers the Eubatus or blackberry group. For this reason our native blackberries have been a puzzle to the ordinary herbarium systematist, and at the same time they have afforded a perfect paradise to the species-maker.

The difficulty of applying the ordinary methods of botanical classification to this group is most clearly seen in the confused and highly inconsistent treatments it has received in the various American as well as European manuals and monographs. The latest edition of Britton's (1)* manual recognizes only 10 species of blackberries growing in northeastern United States and Canada, while Gray's (2) manual which covers somewhat less territory recognizes 30 species besides several varieties and forms. The names of only six of these so-called species appear in both of these standard manuals. Rydberg (3) in his monograph of the North American blackberries recognizes 24 species and 72 hybrids for this same territory. Blanchard, who has for a number of years made a most thorough and extended study of our New England blackberries, published (in 1904-1907) detailed descriptions of 35 species and five varieties of blackberries found in New England. None of these 40 names appear in Britton's second edition of the Illustrated Flora (1913); not even as a synonym. Bailey (4) in his recent treatment of Rubus puts all our New England blackberries into a species-group and coordinates it, by serial numbers, with such European species as *Rubus laciniatus* Willd. and others of equal rank. Our dewberries receive the same harsh treatment, with the exception of *Rubus hispidus* L. which is given specific rank and serial number.

The disagreement among European students of Rubus as to what constitute a species in this genus is equally pronounced. Sudre (5) in his recent monograph of European Rubi illustrates and describes 110 species for all Europe. Rogers (6) lists 100 species of the same genus for England alone.

II. THE OBJECT OF THIS STUDY

The causes of these highly discordant opinions among the students of Rubus concerning the status of its species seem to us to be chiefly the following:

---

*Figures in parenthesis refer to citations at the close of this bulletin.

(*a*) Too great a reliance upon herbarium specimens and a failure to study sufficiently the life history of the growing plants in field and in garden cultures.

(*b*) Failure to appreciate the variations in the supposed specific characters of these plants due entirely to the environmental conditions under which the plants grow.

(*c*) Lack of appreciation of the extent of inter-breeding of the blackberries in the wild and imperfect knowledge of the laws of inheritance, in accordance with which opposed parental characters are transmitted to their hybrid offspring.

In undertaking a critical examination of this sub-genus our aim, therefore, has been to determine as far as possible the origin of these numerous polymorphic forms and their true relationship to one another. In our endeavor to solve this problem we have not only carefully examined all available herbaria material but we have made extensive as well as intensive studies of the plants both in the field and in the experimental garden. We have focused our attention mainly upon New England forms and more especially those found growing in Vermont. The advantages of limiting the field of research to such a restricted area are obvious, while, on the other hand, it is fairly safe to assume that what is true of New England or Vermont blackberries is probably true of blackberries found in other localities.

The present treatise is based upon the results of this study and presents what seems to us to be not only a comparatively simple systematic arrangement of New England blackberries but at the same time expresses very nearly the true relationship of these various forms as they occur in the wild.

III. METHODS USED IN DETERMINING THE SYSTEMATIC RANK OF A GIVEN PLANT

Treatises on the blackberry flora of local or restricted areas prepared by authors who were not sufficiently familiar with the plants in this group in other localities have caused much needless confusion. A large part of the duplication and misapplication of names so common in this species has come about in this fashion as has been pointed out by Sudre (5) and others. In order to forestall such criticism in connection with this article it may be mentioned that the authors have made special efforts to acquaint themselves with the forms of Rubus outside of New England, both native and foreign. Most of the large herbaria in this country have been visited and the plants most carefully studied. The senior author has spent a considerable part of his time for the past 25 years in a critical study of this genus (12, 13). During this time he has travelled and collected plants in nearly every State in the Union. His own herbarium of Rubus is probably as complete as any to be found in this country. For the past seven years the junior author has been associated in this work and has in a similar manner covered most of the Northern and Eastern States. It must also be noted that about 90 percent of the blackberries found in the United States are represented in the New England flora.

On the other hand, our investigations have convinced us that a far greater error has been committed by certain workers, especially in this country, who have relied almost entirely upon a general comparison of dried specimens of plants of this polymorphic group as a basis upon which to determine their systematic rank. There seems to be conclusive proof that some of our ablest systematists are not capable of recognizing the blackberries which they themselves have named and described. This fact alone shows the extreme need of an intensive study of this genus-group. We have, therefore, been compelled to supplement our general observations of this group with a more minute examination of the plants dealt with in order to form a more substantial background for their classification. Such a work, it was hoped, might also add materially to our knowledge of the methods by which new forms (species if you like) originate in the wild. It must also be fundamental to any work which aims at the improvement of horticultural varieties for the reason that nearly all the cultivated forms are native wild plants which have been improved by hybridization or selection, or by both.

The plants listed in the following pages have been critically studied:

1. As to their distribution and development in the wild.
2. As to their behavior in garden cultures and controlled plots.
3. As to the characters of the progeny of supposed natural hybrids.
4. As to the behavior of the progeny of wild forms when artificially crossed.

1. Several stations, especially rich in blackberry forms, scattered over Vermont have been visited at least twice annually for a number of years, the first visit being made when the plants were in flower, the second later in the season when they were in fruit. Herbarium specimens have been collected at these stations for future study and com-

parison, and the distribution of the different forms have been carefully noted. In the case of a natural hybrid the proximity of the two parent species has always been ascertained. The time of flowering of the parent plants, their sterility as shown by their spore and ovule condition, and other factors which determine the probability of such plants hybridizing in the wild have received careful consideration.

Most of the type stations for the new forms of New England blackberries have been visited, the reported species or form generally found growing in that vicinity located and observation made regarding the associated forms. These have served us as a check to the original type specimens of the author who first collected and described them.

Seasonal differences in form and variations due to environmental factors such as shade and sunlight, humidity, altitude, water contents of the soil, etc., have been carefully noted and interpreted as far as such general observations of plants grown under such uncontrolled conditions would safely permit.

2. Specimens of nearly all forms of blackberries that have been reported from Vermont and a few from outside the State have been collected and transplanted to the experimental garden. By a comparison during the entire growing seasons for seven years of about 60 different forms growing side by side and under almost identical environmental conditions, it has been possible to correct many nomenclatorial errors which have found their way into the systematic literature of Rubus. One case may be cited as an illustration. *R. frondosus* Bigelow and *R. recurvans* Blanchard have been considered by most American authors as two distinct species. The most important character used in distinguishing between these two supposed species is the leafy-bracted inflorescence of *R. frondosus* and the more or less lack of such leafy bracts in *R. recurvans.* Our garden cultures have shown that where these two plants are grown side by side there is very little difference in the amount of the leafy bracts. It has also been shown that the leafy bracts are present in both plants if grown in the shade while a more or less lack of such leafy bracts results if grown in the sunlight. This character, therefore, cannot be relied upon as a specific character and we must consider *R. recurvans* as a mere form of *R. frondosus* in view of the fact that the latter name antedates the former.

The effects of environmental factors upon the vegetative characters of a few wild forms have been tested by growing several shoots from the same plant in plots under greenhouse conditions, where such factors as soil temperature, air temperature, humidity and light could be definitely controlled and measured. Continuous records of these factors in the different plots were kept for several months and the corresponding plants compared. Plate II shows two corresponding similar shoots of plant No. 7-2 *R. allegheniensis* × *frondosus* grown under different conditions. The difference in the size and number of prickles and in the number of glandular hairs on the two shoots is marked. How easy might it not be for the herbarium systematist to make two species of this one plant!

3. Seedlings of about 50 wild forms, mostly suspected hybrids, have been grown and in several cases indisputable evidence of the hybrid origin of the parent plant have been obtained by the more or less complete reversion of the seedlings to the parent species. The most striking examples of such reversions are shown in such forms as *R. trifrons* Blanchard, *R. groutianus* Blanchard, *R. allegheniensis* × *frondosus* and *R. allegheniensis* × *canadensis*. Plate III, figs. 1 and 2 show two seedlings of plant No. 122-1 *R. allegheniensis* × *frondosus*, selected to illustrate segregation in the shape of the leaf.

4. More than 30 different crosses have been effected artificially between the different wild forms, and the resulting plants are at present under observation in the plant breeding gardens of the station. In general the characters of these seedlings are intermediate between those of the two parents, although some of these hybrid plants show a greater resemblance to the mother than to the father plant. Some of these first generation plants are almost exact duplicates of the corresponding hybrids found in the wild.

IV. HYBRIDITY AMONG AMERICAN RUBI

No matter which of the several proposed theories we accept as a satisfactory explanation of the evolutionary differentiation of the organic world in general, we must admit that as far as the Rose family is concerned, and more especially the genus Rubus, numerous new forms are at present being produced in the wild through hybridization. Evidences of the hybrid origin of many American blackberries are so frequent and so convincing that no thorough student of Rubus will question its occurrence. It seems to us that it is no longer a question of whether or not new species of blackberries are produced in the wild through natural hybridization but rather that it is a question whether hybridization is not the primary or only factor in the production of new species within this group. If new forms are developed by natural hybridization within the genus Rubus—an inference which the evidence at hand supports—it may be that it is also a very important factor in the evolution of plants within other groups, as has already been suggested by Lotsy (*7*) and others.

Although a more detailed discussion of the subject of spontaneous hybridization will be soon published it may not be amiss to enumerate briefly some of the more important facts which have led to the conclusion that inter-crossing between the different species of blackberries in the wild is of common occurrence.

1. All New England forms of blackberries show a more or less degree of infertility. In all our search for new forms we have yet to find a blackberry that is 100 per cent fertile. On the other hand, we have had under observation for the past seven years several colonies in the field as well as numerous individual plants in the gardens of the plant breeding station which during this time have matured only a few scattered drupelets or none at all, although the seasons have been favorable for fruit production. This infertility is largely due to the impotency of the pollen; a character which Jeffrey (8, 9, 10) and others claim is present only in plants of hybrid origin. The pollen condition of the New England blackberries shows a very wide range of variation. For instance, in *R. allegheniensis* Porter the percentage of morphologically perfect pollen is about 96, while that of *R. hispidus* L. is less than 10 (plate IV). Between these two extremes exists all grades of intermediacy. This sterility or partial sterility of all plants within this group is at least suggestive of their hybrid origin.

2. Intermediate forms between all of the well recognized species exist in the wild. In the same field one may often find a colony of perfectly typical *R. hispidus* L. and a few rods distant another colony of equally typical *R. setosus* Bigelow, and also there may be half a dozen other colonies quite different from each other and yet all intermediate between these two fairly well marked species. This situation is to be found in nearly any other two closely related species of Rubus. The presence of these many intermediate forms can be logically accounted for if we assume that the two species interbreed.

3. It will be noted that wherever there is found an intermediate between any two forms of blackberries one can usually locate the two suspected parents in close proximity. At every station for *R. permixtus* Blanchard visited by us, we have not failed to find *R. hispidus* L. and *R. allegheniensis* Porter growing in the vicinity. This is equally true of any other intermediate form listed in the following pages as a hybrid. Such circumstantial evidence confirms our belief in their bastard origin.

4. Plants of the blackberry sub-genus are very variable. This characteristic of the group is familiar to all students of Rubus. Their vegetative structures are greatly modified by the conditions under which they grow (plate V). In fact, the perfect chaos now existing in the systematic literature is largely due to the misinterpretation of these purely vegetative variations. Since students of evolution are almost unanimous in their assertions that hybridization increases variation in vegetative characters, it may be inferred that the reverse also is true; that vegetative variation is an index of hybridization.

5. Seeds from the selfed flowers of a number of suspected hybrids have been grown and these plants in the majority of cases show a reversion to the supposed parent types (plate III), which of itself, to our mind, is a positive proof of hybrid origin.

6. A number of artificial crosses have been effected between different species, a detailed account of which will be published soon. The plants from these crosses are almost identical with the suspected wild hybrids. It therefore seems reasonable to assume that the wild forms have had a similar origin.

7. In more than 30 different combinations of New England blackberries that were cross pollinated, not one failed to produce viable seeds. This would indicate that they are all capable of cross-fertilization if given a chance.

The only logical conclusion that can be drawn from such evidence is that at least New England blackberries hybridize in the wild and that this occurs quite frequently.

In considering the hybrids of Rubus we must not overlook the fact that nearly all specific characters in this genus are quantitative and not qualitative characters. One species of blackberry may differ from another species in the width of its leaflets, in the amount of pubescence, in the erectness of cane, in the length of inflorescence, etc. It is nearly always a question of a more-or-lessness of the particular characters which distinguish it from the other plants of this group. A hybrid, therefore, will nearly always show an intermediacy in the characters which are present in varying degrees in both of the parents, and besides, these compromise characters will also possess the characters in diminished form which are present in only one of the parents. The offspring of such a hybrid as a rule will not show a segregation into pure dominants and recessives in the ordinary Mendelian ratio. On the other hand there will be found all grades of intermediates. This is characteristic of a blend inheritance. Whether or not these intermediate forms can be accounted for by the Nilsson-Ehle hypothesis we do not know. Even in some cases, as in *R. permixtus* Blanchard, *R. frondisentis* Blanchard and *R. abbrevians* Blanchard, these hybrids appear to be more or less fixed.

V. HYBRIDITY AS IT AFFECTS CLASSIFICATION

The student of evolution, who wishes to express the true relationship of the various forms which he finds in such a polymorphic genus as Rubus, is very much embarrassed in coordinating his facts with any acceptable scheme of classification. In order to avoid adding new specific names to the already long and cumbersome lists such terms have been employed as sub-species, varieties, forms, etc. These, however, in many cases do not express the genetic relationship of the plants thus designated.

Sudre (5) in his monograph of European Rubi uses the term "species-group" to designate a number of closely allied forms consisting generally of one primary or dominant species and a large number of subordinate forms which he terms "species of the second order," "species of the third order," "varieties," "forms," etc. Such use of a binomial to designate a collective species is very unfortunate, although it has obvious advantages from the systematic point of view. A hybrid between two collective species would have no place in such a scheme but would in most cases be placed in an entirely different species-group. For instance, *R. permixtus* Blanchard by such a treatment would be grouped with *R. setosus* Bigelow where it does not belong. It is very probable that many of Sudre's subordinate forms are hybrids.

It must be admitted that the number of forms included in a species will depend largely upon the author's conception of a species as well as upon the importance he assigns to a certain character. Nevertheless there are some forms that stand out prominently from all the closely allied forms, differing from them in one or more well-marked characters. These, if they breed "true to type," should be considered valid species even if they are remote crypto-hybrids. Other forms that unquestionably are of recent hybrid origin should be designated as such by a combination of the specific names of their parents or suspected parents.

VI. THE NEW ENGLAND BLACKBERRIES

New England blackberries do not differ very much from blackberries grown in other parts of the world. They have perennial roots and biennial, woody stems; the stems develop the first year and die the second year after flowering and fruiting. The stems range from weak trailers to erect canes from two to three meters high. Their leaves are palmately compound, having as a rule five more or less stalked leaflets, but in some of the dewberry types those of the second year's cane as well as of the first year's cane are trifoliolate or even unifoliolate. Their flowers are borne on more or less contracted cymose-racemes, the terminal flower opening first. The fruit consists of partly cohering drupelets which at maturity break off with the fleshy receptacle. The canes, leaves and inflorescence are variously covered with simple hairs, gland-tipped hairs and prickles.

In considering the specific characters of the blackberries it must be kept in mind that their canes are of two kinds: the first year's cane or turion and the second year's cane which bears the flowers and fruit. Any complete herbarium specimen, therefore, should include a turion mounted so as to show both surfaces of the leaflets, a portion of the old cane showing the inflorescence and a similar portion collected later in the season showing the mature fruit. With any of the above mentioned parts lacking it is not easy to identify a specimen with any degree of certainty. The turions vary from stout, erect, somewhat drooping canes to weak, prostrate runners; these in late fall show a more or less tendency to root at the tip and propagate the plant vegetatively in this way. The canes are terete as in the dewberry types or they may be more or less grooved or furrowed, the amount varying somewhat with the age of the cane. The alternate leaves in the high-bush forms are palmately compound and are generally 5-foliolate; in the dewberry forms 3-foliolate. The leaflets are either perfectly glabrous or are covered more or less with simple hairs and in some of the pubescent forms with gland-tipped hairs along the veins. The amount of pubescence varies somewhat with the season's growth. The stems, petioles, petiolules and larger veins are covered in divers ways with prickles and gland-tipped hairs, these varying greatly in size and shape in the different species, or they may be almost devoid of prickles and hairs of any kind, as in *Rubus canadensis* L.

The fruiting canes while living retain to a large extent their turion characters. But the second year's growth, which is always axillary, may differ widely from the first year's growth in the shape and size of the leaflets, amount of pubescence and in other respects. The branches may be long and leafy and terminated by the inflorescence or they may consist merely of a short cymose-raceme subtended by a few leaves. The leaves are mostly 3-foliolate. Their shape, surface covering, serrations, etc., vary as widely as do the same characters of the leaves on the turions. The inflorescence varies from a few-flowered corymb-like arrangement of the flowers as in the dewberry types to an elongated raceme-like arrangement as in most of the high-bush forms. Although this type of inflorescence for the sake of brevity may be referred to in the following pages as either a raceme or a corymb, it must be understood that in all blackberries and dewberries alike the inflorescence is a false raceme, in spite of numerous statements in current literature to the contrary (see Card's Bush-Fruits; also Bailey's Evolution of Our Native Fruits) (14). The terminal bud opens first while the remaining buds open in the order of a true raceme. The flowers in all New England forms are white or cream colored. The rachis and pedicels may be either smooth and glabrous or variously covered with prickles, gland-tipped hairs and simple hairs. The fruit consists of few to many partly coherent drupelets which break off with the fleshy receptacle when mature. Its color varies from jet black to purple and red, amber-colored albino forms occurring in some species.

As has been pointed out, the blackberries are conspicuous for the characters which they have in common rather than for those which enable us to distinguish one form from another. The characters used in differentiating between the different species are nearly always relative characters. The dewberries tip profusely late in the season; but it must be noted that all New England forms of blackberries tip if their turions touch the ground. The inflorescence of the dewberries resembles that of a cymose-corymb while in most of the high-bush forms the flower cluster resembles more nearly a raceme; but the general plan of all is that of a false raceme. Moreover, all New England forms have simple hairs, gland-tipped hairs and prickles in varying amounts; even the smooth, glabrous, eglandular, unarmed form of *Rubus canadensis* L. possesses these structures in rudimentary form. If these protodermal outgrowths are not noticeable in the mature plants they are at least present in the very young seedlings. In fact, it is very difficult to select a single character possessed by one form or species of blackberry which is not common to all New England forms in varying degree.

The blackberries of New England are distributed from the highest mountain peaks to the lowest valleys. They are adapted to growing in the open. *Rubus canadensis* L. is practically the only species that is found growing in dense forests. They are especially prolific in alluvial soils which have been cleared of their forest trees. Here in open pastures, along stone walls and in abandoned fields they have found a congenial soil in which to grow and multiply.

There are three fairly well marked groups of New England blackberries; each group including four valid species. *R. allegheniensis* Porter, *R. argutus* Link, *R. pergratus* Blanchard and *R. frondosus* Bigelow comprise the first or high-bush group. These species have erect canes and pubescent leaves. In striking contrast to these high-bush forms is the dewberry group which includes *R. hispidus* L., *R. flagellaris* Willd., *R. enslenii* Tratt. and *R. baileyanus* Britton. These species have trailing stems, trifoliolate leaves and corymbose-like inflorescence. Somewhat intermediate between these two groups and yet quite distinct from either of them are the semi-erect species which include *R. setosus* Bigelow, *R. vermontanus* Blanchard, *R. elegantulus* Blanchard and *R. canadensis* L. These have glabrous leaves and canes. All other forms of blackberries found in New England can be accounted for by the inter-crossing of these twelve species. Plate VI shows in a diagramatic way the parentage or suspected parentage in some cases, of these various New England forms.

In the descriptions and keys which follow our aim has been to give only the marked or differentiating characters for that particular species or hybrid.

KEY TO THE TWELVE SPECIES OF NEW ENGLAND RUBUS § EUBATUS

a. Stems erect, or ascending and recurving; leaves on new canes mostly 5-foliolate* *b.*

b. Leaves of early summer densely short-villous or velvety on the lower surface *c.*

c. Short gland-tipped hairs abundant; seeds 2 mm. long; racemes about 14-18-flowered .... **R. allegheniensis,** 23.

c. Gland-tipped hairs and bristles absent; seeds 2½ mm. long†; racemes 8-12-flowered *d.*

d. Terminal leaflet on new canes oval or oblong-ovate *e.*

e. Prickles on stem 5-7 mm. long with broad base; at least lower pedicels armed with small hooked prickles, **R. argutus,** 27.

e. Prickles on stem 2-4 mm. long, about 6 to the dm.; pedicels unarmed .... **R. pergraus,** 29.

d. Terminal leaflet on new canes suborbicular or broadly ovate.

---

*At high altitudes occurs a form of *R. setosus* with leaves mostly 3-foliolate and stems often reclining.

†In bulk, or weight, twice as large as in *R. allegheniensis*, i. e. $(2)^3 : (2\frac{1}{2})^3$.

Bracts of raceme nearly all leafy; leaflets short, acuminate, **R. frondosus,** 31.

b. Lower surface of leaves glabrous *g.*

g. Gland-tipped hairs and bristles absent *h.*

h. Prickles absent from stem, or rudimentary, **R. canadensis,** 35.

h. Prickles of the stem needle-like with broad, flattened base, about 4 or 5 to the cm....**R. elegantulus,** 37.

h. Prickles of the stem setaceous, about 20 to the cm., **R. vermontanus,** 39.

g. Gland-tipped bristles abundant on stem, petiole, raceme and calyx; stem beset also with stronger glandless bristles curving downward, about 40 to the cm., **R. setosus,** 41.

a. Stems trailing; leaves on new cane mostly 3-foliolate *j.*

j. Stems and petioles armed with many slender reflexed bristles, **R. hispidus,** 43.

j. Stems and petioles armed with stiff prickes 1-3 mm. long, 1-5 to the cm.; pedicles few, erect, elongate *k.*

k. Leaves somewhat sharply serrate, slightly hairy beneath, especially the veins; prickles curved; pedicels usually 2-5, **R. flagellaris,** 45.

k. Leaves with coarse broadly rounded mucronate teeth, pubescent beneath; pedicels 1-3; these and the stems often with stalked or sessile glands ....**R. baileyanus,** 49.

k. Leaves glabrous beneath, ciciolate; prickles minute and few; pedicels often only one, eglandular..........**R. enslenii,** 47.

KEY TO SOME NEW ENGLAND HYBRIDS AND BLEND SPECIES OF RUBUS § EUBATUS

a. Stems erect, or ascending and recurving *b.*

b. Leaves of early summer velvety or somewhat pubescent on lower surface *c.*

c. Stems and inflorescence bearing gland-tipped hairs or bristles *d.*

d. Terminal leaflets on new cane oval or oblong-ovate *e.*

e. Pedicels armed with pungent hooked prickles, **R. allegheniensis X argutus,** 53 **(R. andrewsianus).**

e. Pedicels without hooked prickles *f.*

f. Petioles on new cane beset with gland-tipped hairs *g.*

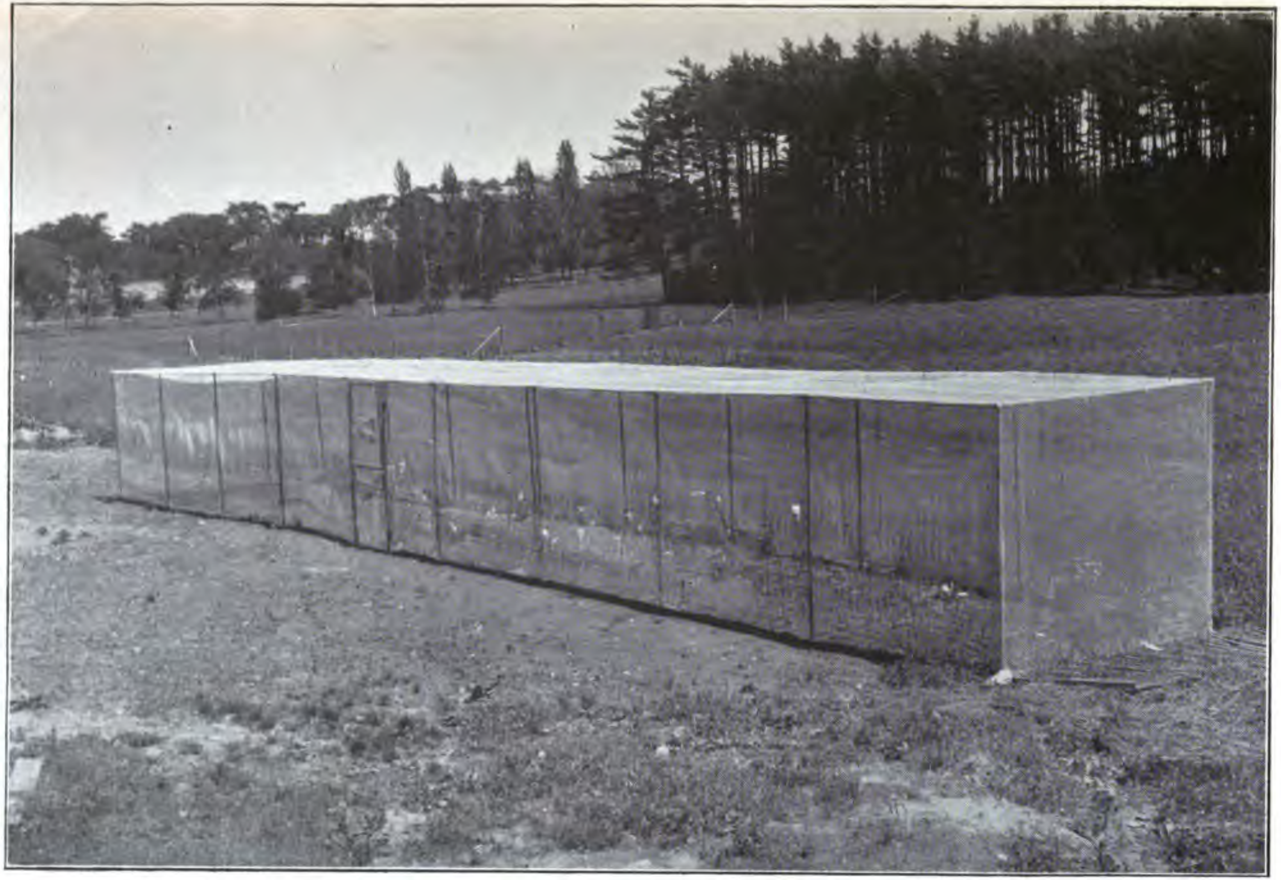


Plate I

Cage in which the twelve species of New England blackberries were grown.

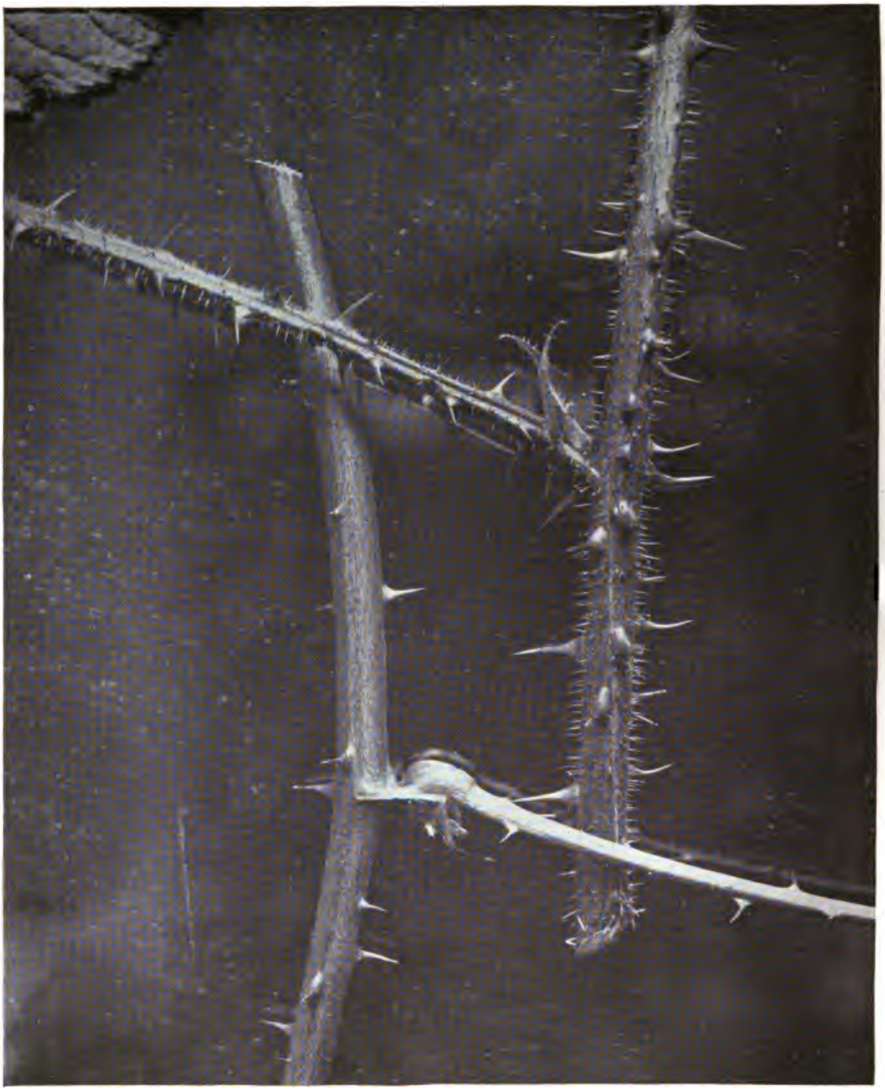


PLATE II

Rubus allegheniensis X frondosus

Two shoots from the same plant grown under different external conditions. The cane shown on the left (glandular one) is the third node of a shoot which grew in a plot having a high temperature, a low humidity and full sunlight. The cane shown on the right (glandular one) is the third node of a shoot which grew in a plot having a comparatively low temperature, a high humidity and the plants were shaded by three layers of cheesecloth.

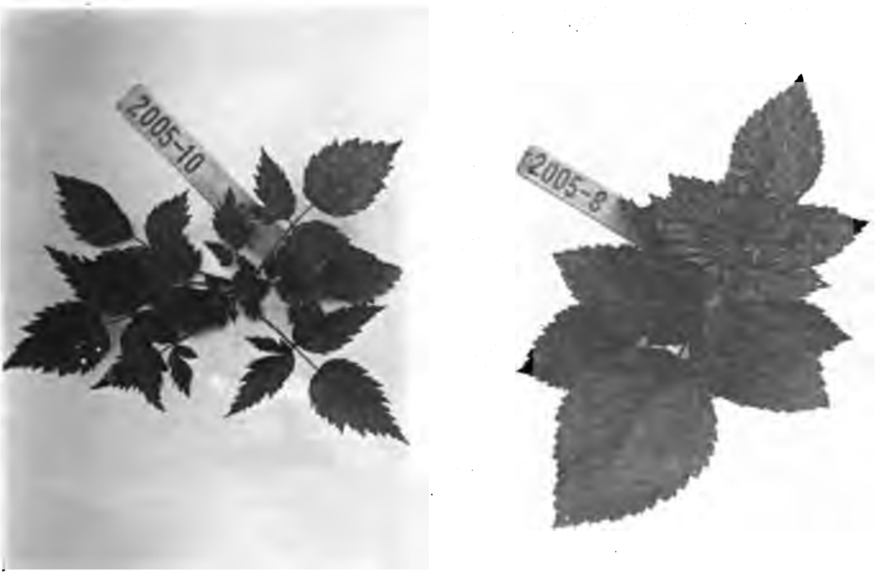
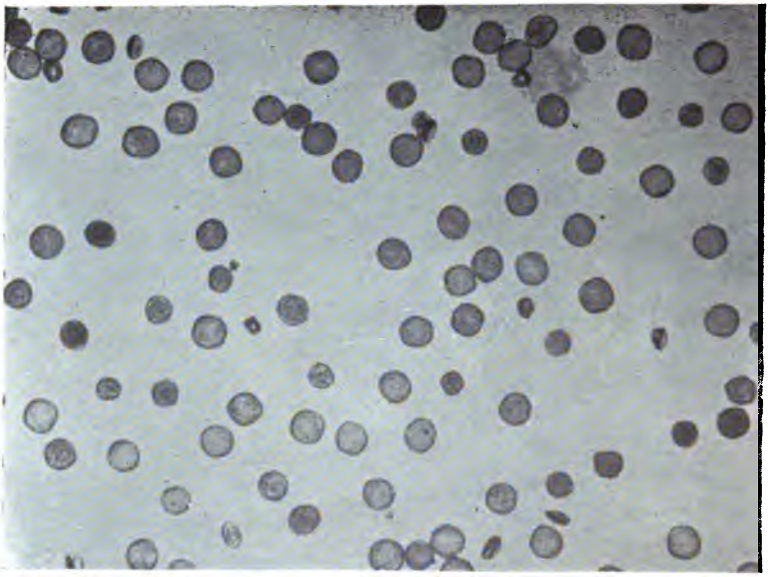


PLATE III

Rubus allegheniensis X frondosus

Two seedlings from selfed flowers of Plant No. 122-1 showing reversions to the parent types. Plant No. 2005-8 shows a reversion towards *R. frondosus* Bigelow in the orbicular shape of its terminal leaflet. Plant No. 2005-10 shows a reversion toward *R. allegheniensis* Porter in having a narrow, ovate terminal leaflet.



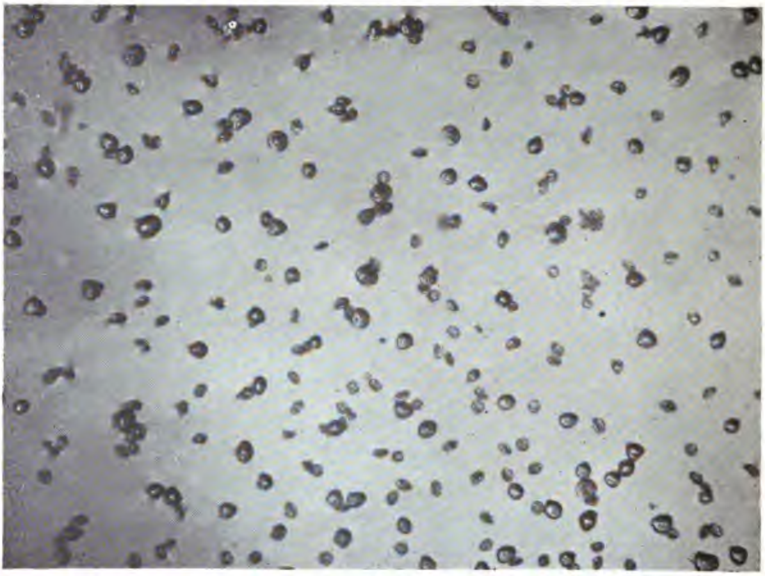


PLATE IV

Figure 1. A microphotograph of the pollen grains of *R. allegheniensis* Porter, X 100. About 96% morphologically perfect grains and considered "good pollen."

Figure 2. A microphotograph of the pollen grains of *R. hispidus* L. X 100. Less than 10% morphologically perfect grains and considered "poor pollen."

g. Cane and inflorescence sparsely beset with gland-tipped hairs and prickles............ **R. allegheniensis X canadensis (R. orarius).**

g. Cane and inflorescence copiously beset with gland-tipped hairs and prickles *h.*

h. Racemes 8-11-flowered, short cylindrical; seeds 2½ mm. long ....**R. pergratus X setosus,** 63 **(R. frondisentis).**

h. Racemes 14-18-flowered, elongate; seeds 2 mm. long ....**R. allegheniensis X setosus,** 61 **(R. glandicaulis).**

f. Petioles on new cane glandless, copiously armed with hooked prickles *i.*

i. Prickles on new canes with broad, flattened base; petals about 1½ cm. long; racemes elongate, **R. allegheniensis X elegantulus,** 57 **(R. flavinanus).**

i. Prickles on new cane setaceous; petals about 1 cm. long; racemes cylindrical, **R. allegheniensis X vermontanus,** 59 **(R. fraternus).**

d. Terminal leaflets on new cane broadly ovate *j.*

j. Prickles on stems setaceous, **R. frondosus X setosus,** 65 **(R. abbrevians).**

j. Prickles on stems stout, 3-5 mm. long, **R. allegheniensis X frondosus.**

c. Stems and inflorescence without gland-tipped hairs or bristles *k.*

k. Terminal leaflet on new cane broadly ovate; pedicels armed, **R. argutus X frondosus,** 55 **(R. jeckylanus).**

k. Terminal leaflet on new cane oval or ovate; pedicels unarmed ....**R. canadensis X pergratus.**

b. Leaves glabrous on the lower surface *l.*

l. New cane bearing gland-tipped hairs *m.*

m. Pedicels mostly 1-2 cm. long; cane slender, **R. setosus X vermontanus (R. vermontanus** var. **viridifolius).**

m. Pedicels mostly 2-5 cm. long; cane stout, **R. canadensis X setosus,** 67 **(R. junceus).**

l. New cane without gland-tipped hairs *n.*

n. Prickles of the stem remote, 1 or 2 to the cm., **R. canadensis X vermontanus.**

n. Prickles of the stem numerous, about 20 to the cm., **R. elegantulus X vermontanus.**

n. Prickles of the stem very numerous, about 50 to the cm., **R. elegantulus X setosus (R. groutianus).**

a. Stems prostrate (new shoots sometimes ascending but soon reclining and trailing) *o.*

o. Stems and inflorescence bearing gland-tipped bristles *p.*

p. Leaves of early summer velvety on the lower surface *q.*

q. Terminal leaflet orbicular; racemes 1-10-flowered, lower flowers leafy-bracted .....**R. baileyanus X frondosus,** 75 **(R. arenicola).**

q. Terminal leaflet elongate; racemes many-flowered, lower flowers not leafy-bracted *r.*

r. Prickles hooked; glandular hairs of uniform length, **R. allegheniensis X flagellaris,** 71 **(R. elongatus).**

r. Prickles straight; glandular hairs of unequal length, **R. allegheniensis X hispidus,** 69 **(R. permixtus).**

p. Leaves glabrous *s.*

s. Stems without prickles, beset with numerous recurved bristles ....**R. hispidus X setosus,** 77 **(R. trifrons) (R. jacens).**

s. Stems with bristles and slender prickles, **R. hispidus X vermontanus (R. cubitans).**

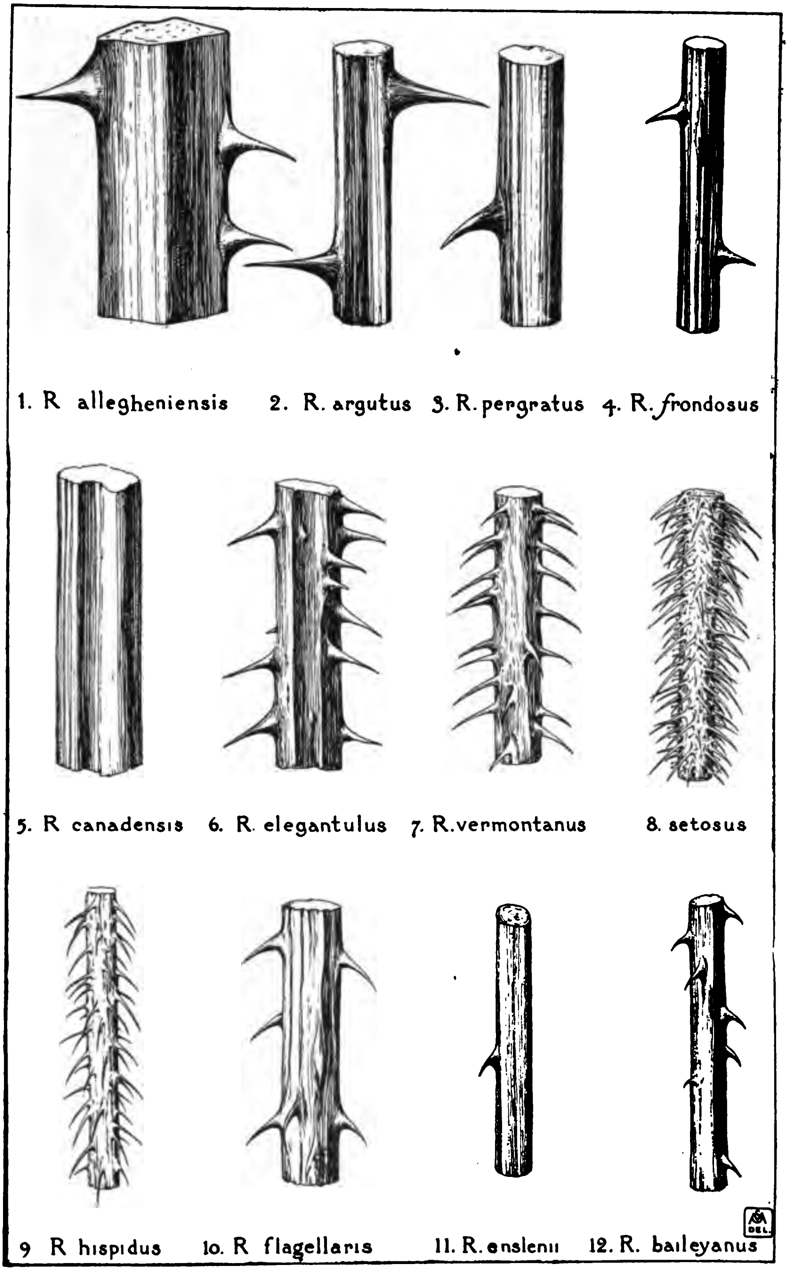
o. Gland-tipped hairs and bristles absent *t.*

t. Leaves on new cane mostly 3-foliolate, **R. baileyanus X flagellaris,** 79.

t. Leaves on new cane mostly 5-foliolate *u.*

u. Prickles large, hooked; pedicels armed, **R. argutus X flagellaris,** 73 **(R. multispinus).**

u. Prickles slender, straight, pedicels unarmed, **R. flagellaris X frondosus (R. plicatifolius).**



1. R allegheniensis 2. R. argutus 3. R. pergratus 4. R. frondosus

5. R canadensis 6. R. elegantulus 7. R. vermontanus 8. setosus

9 R hispidus 10. R flagellaris 11. R. enslenii 12. R. baileyanus

PLATE I

Drawings showing the stem character of the twelve species of New England blackberries. Redrawn from photograph. Natural size.

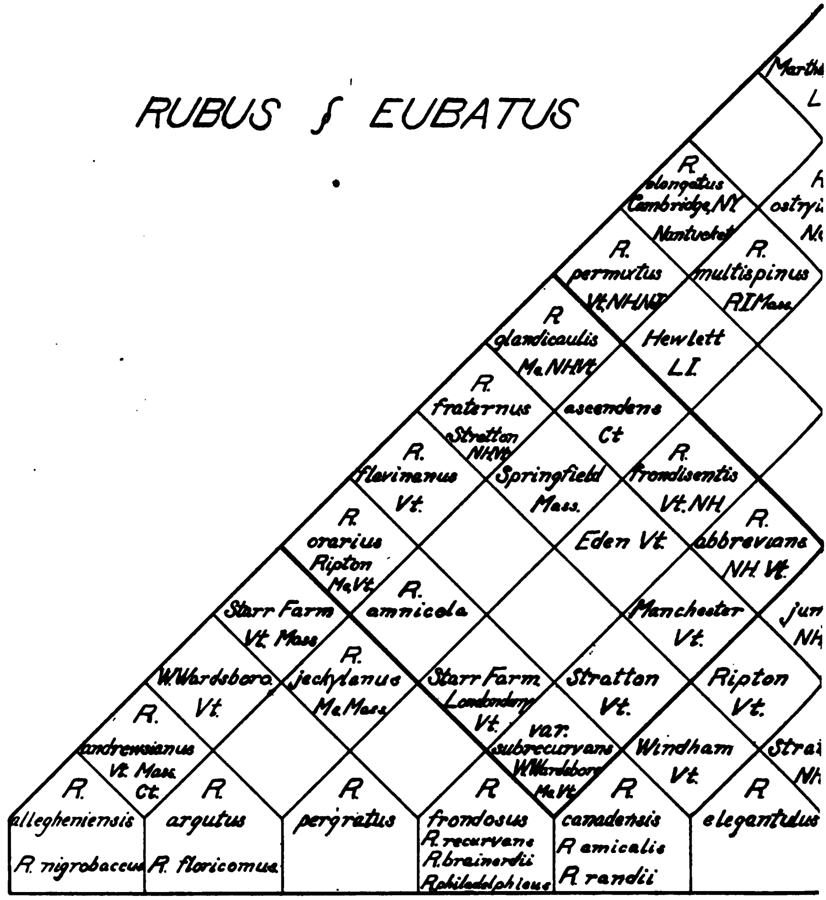
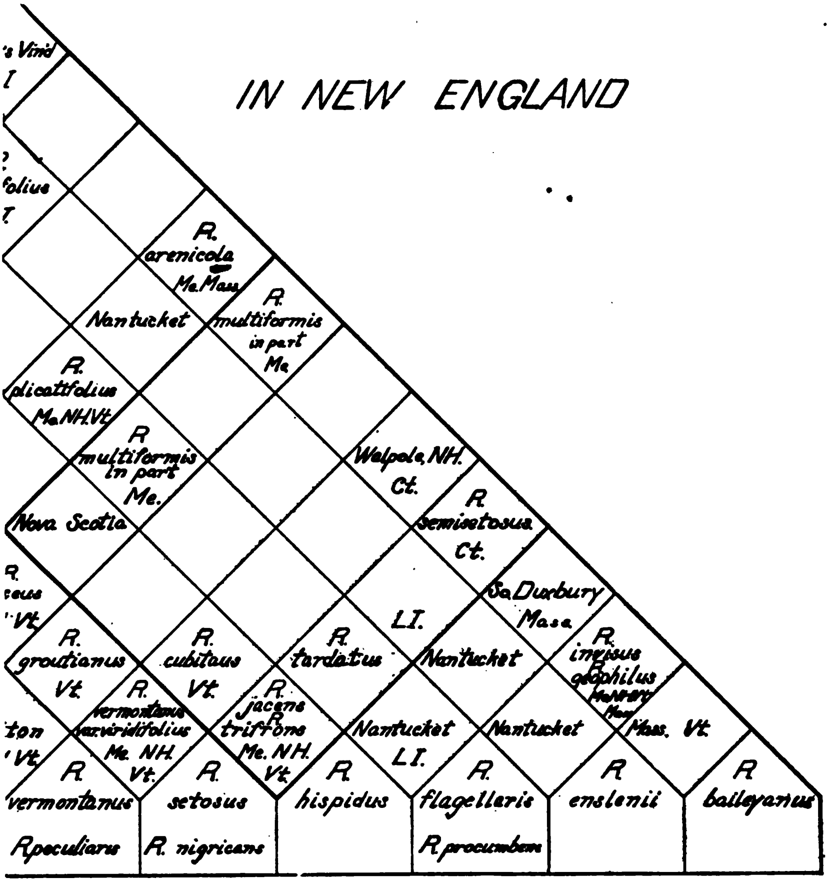


PLATE VI

A diagram showing the systematic arrangement of New England blackberries. The names appearing in bold type in the lower part of the diagram are the twelve valid New England species together with their synonyms which are shown in smaller type. In the squares above are indicated the hybrids



or suspected hybrids which have been found in New England and in most cases the States in which they were found are also indicated.

The synonym of such hybrids, whenever there are such, are also indicated in the same square. Thus *Rubus allegheniensis X elegantulus* occurs in Vermont and has been described as *Rubus flavinanus* Blanchard.

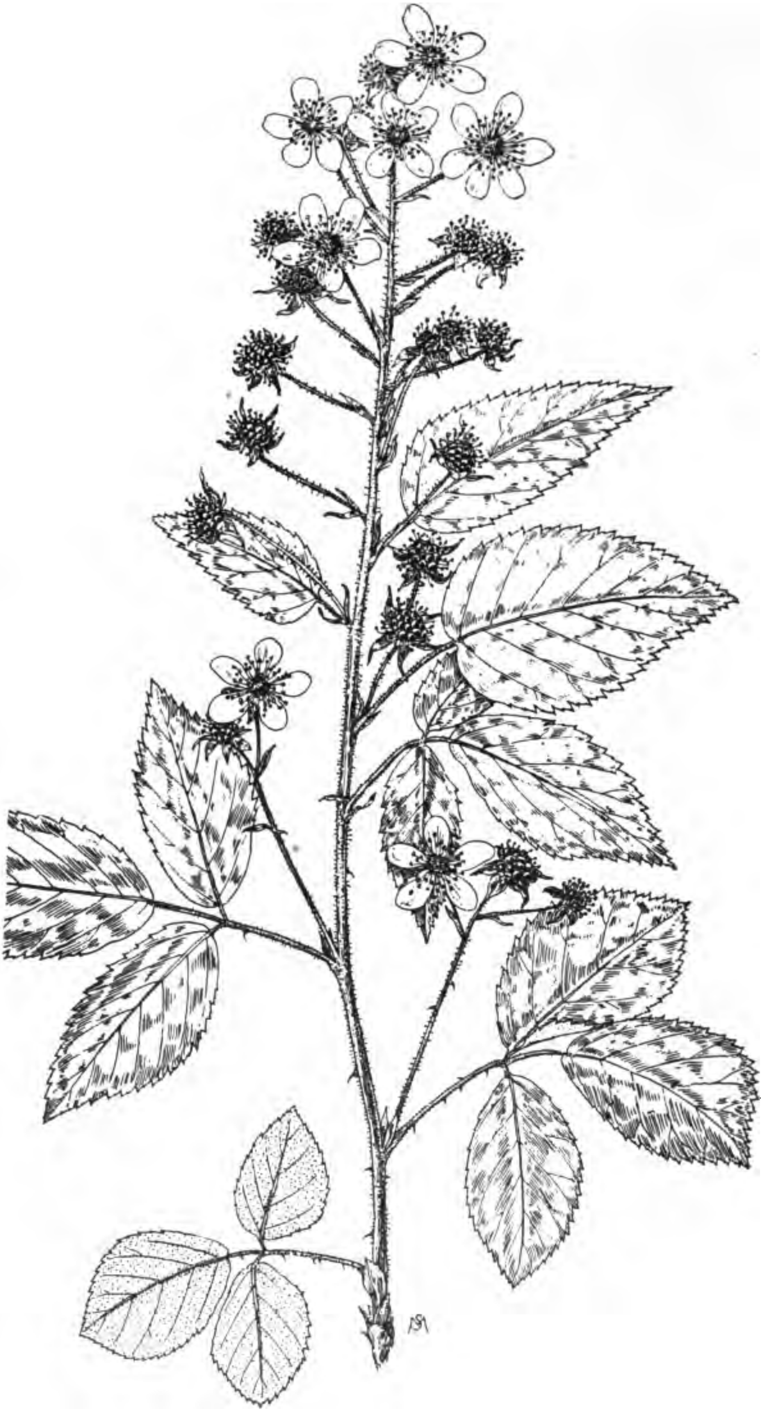


PLATE VII

R. allegheniensis Porter

Two-thirds natural size. Raceme of plant from Chipman Hill, Middlebury, Vt.

HIGH-BUSH BLACKBERRY

Rubus allegheniensis Porter, Bull. Torrey Club 23: 153. 1896
Rubus villosus montanus Porter, Bull. Torrey Club 17: 15. 1890
Rubus montanus Porter, Bull. Torrey Club 21: 120. 1894. Not
  R. montanus Ortman. 1852
Rubus nigrobaccus Bailey, Evol. Nat. Fr. 379. 1896

Stems erect, sometimes reddish, armed with stout, straightish prickles; stems and pedicels glandular-pubescent; leaves on turions mostly 5-foliolate, of early summer densely villous above, velvety beneath; racemes about 14-18-flowered; drupelets small; berries thimble-like and possessed of a peculiar spicy flavor; seeds about 2 mm. long.

Pollen only about 5% imperfect. Seedlings show little or no segregation in culture.

Time of blooming: May 28 to July 4.

Time of fruiting: August 10 to September 20.

Type station: Pocono Summit, Pa.

Distribution: Dry thickets and recent clearings throughout New England.

This is one of the purest and most distinct species of our New England blackberries. In the wild it shows quite a range of variation in color of stem, ranging from reddish to a pale green, and in the number and size of prickles and glandular hairs but these variations are largely due to environmental conditions under which it grows. An albino form also occurs. This plant was recognized by Porter who first described it as a mountain form of *R. villosus* Ait., but it must be borne in mind that what Porter then considered *R. villosus* was the "common high-bush blackberry" of Pennsylvania, *R. argutus* Link. So by way of contrast he called his plant a mountain form while in New England it constituted our common lowland blackberry.

Although this species is not represented by any of our cultivated varieties on account of its small and seedy fruit, its apparent hybrids with other wild species are very closely related to such horticultural varieties as: Ancient Britton, Badger, Dorchester, Eldorado, Lovett, Taylor, Agawam, Barnard, Erskine Park, Jumbo, Lawton, Snyder, Stone and Wachusett.

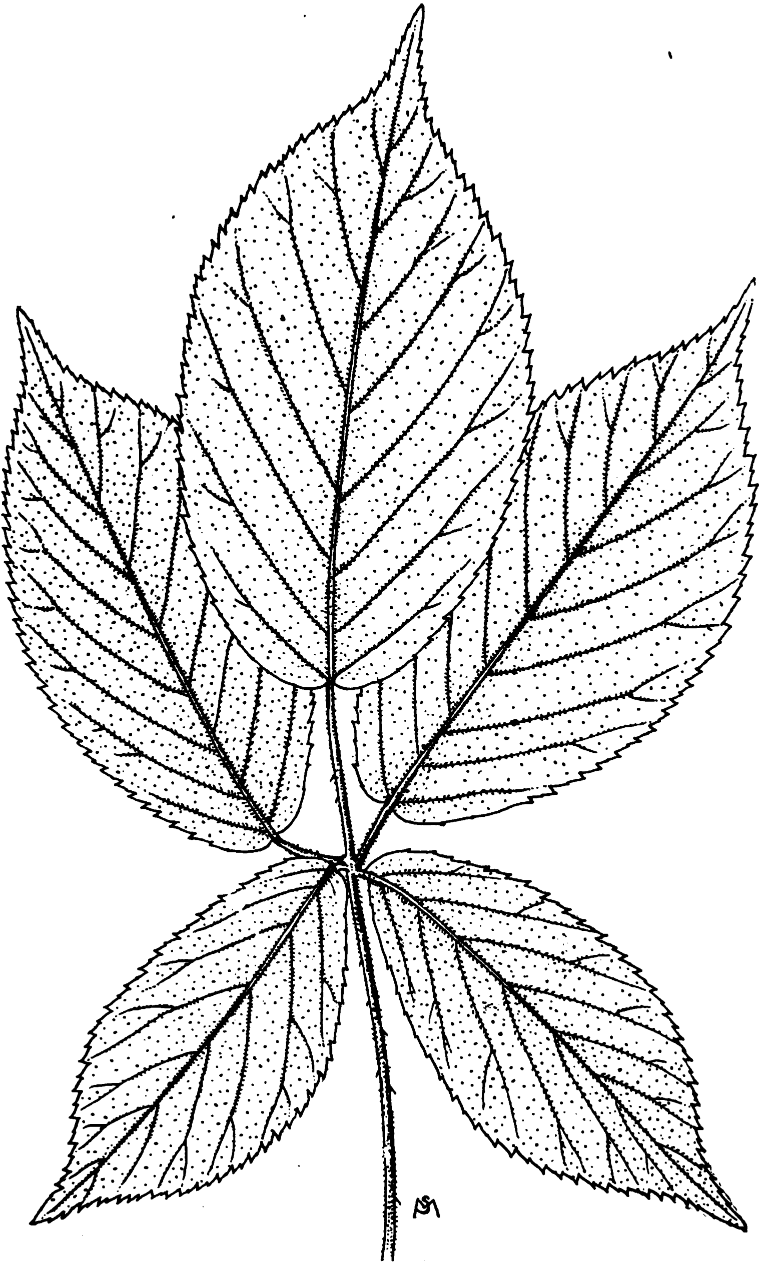


PLATE VIII

R. allegheniensis Porter

Four-fifths natural size. Leaf.

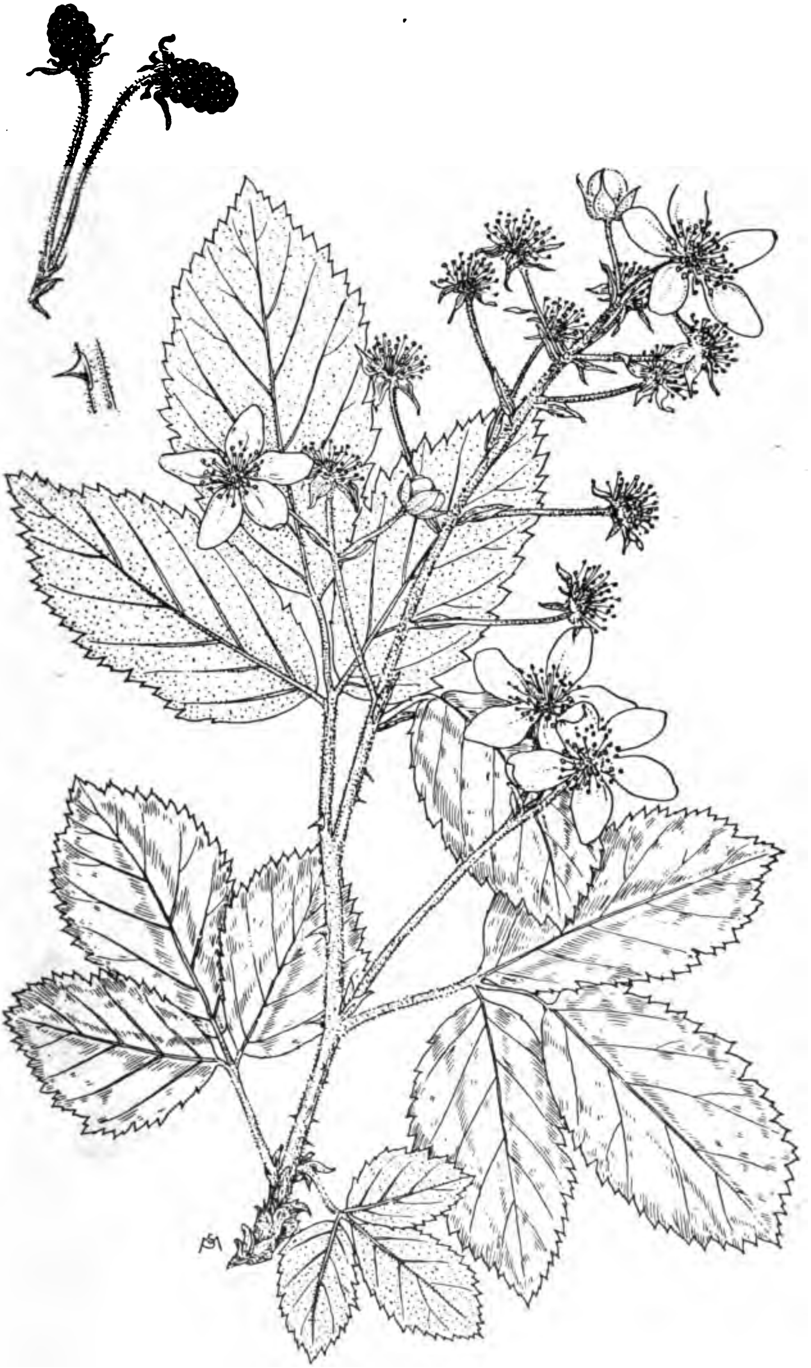


PLATE IX

R. allegheniensis Porter

Four-fifths natural size. Raceme and fruit from pubescent form.

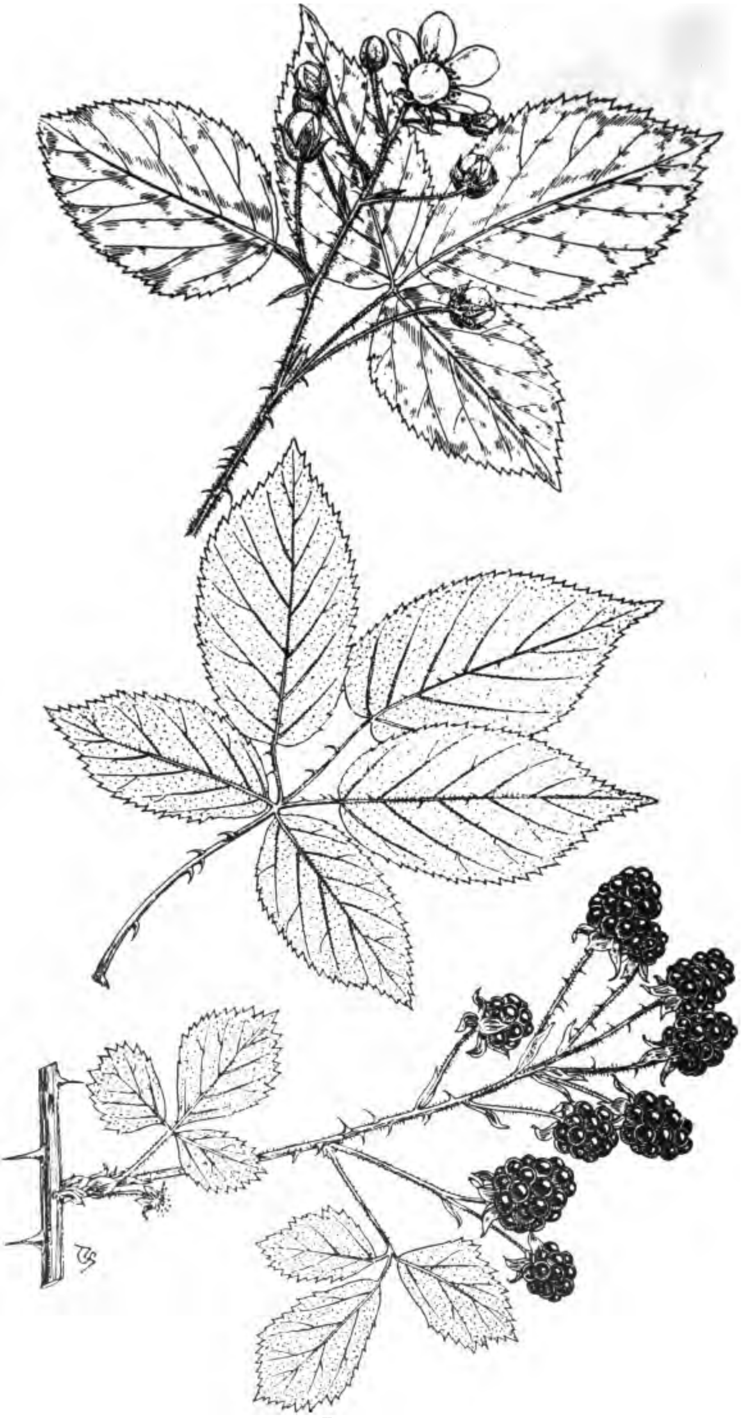


PLATE X

R. argutus Link

Two-thirds natural size.

TALL BLACKBERRY

Rubus argutus Link, Enum, Hort. Berol. 2: 60. 1822
Rubus floricomus Blanchard, Am. Bot. 9: 106. 1905

Stems erect, deeply furrowed, glabrous, armed with prickles, 5-7 mm. long with a broad base; leaves on turions mostly 5-foliolate, in early summer densely short-villous beneath; petioles, petiolules and midveins somewhat pubescent and armed with stout usually hooked prickles; racemes 8-12-flowered; at least lower pedicels armed with small hooked prickles; drupelets about 30; seeds large, about 2½ mm. long.

Pollen about 20% imperfect.

Time of blooming: May 24 to July 1.

Time of fruiting: August 8 to September 21.

Type station: "North America."

Distribution: On dry grounds at low altitudes in southern New England.

Link's short but concise description and a careful examination of several leaves of the type specimen convinces us that Link's type is identical with the common high-bush blackberry of the central United States which is correctly figured and described in Britton's Ill. Fl., Vol. 11, p. 202, 1st ed., as *R. villosus* Ait., and as *R. argutus* Link in 2nd ed., p. 280, fig. 2301. It ranges from southern New England to North Carolina westward to the Mississippi. Appears constant throughout this territory but hybridizes freely with other species. An albino form also occurs.

Cultivated varieties whose probable progenitor is *R. argutus* are: Clyde, Dallas, Eric, New Rochelle, Tree Blackberry, Wallace and White Blackberry. Its crosses with *R. frondosus* Bigelow and *R. allegheniensis* Porter are also horticulturally important.

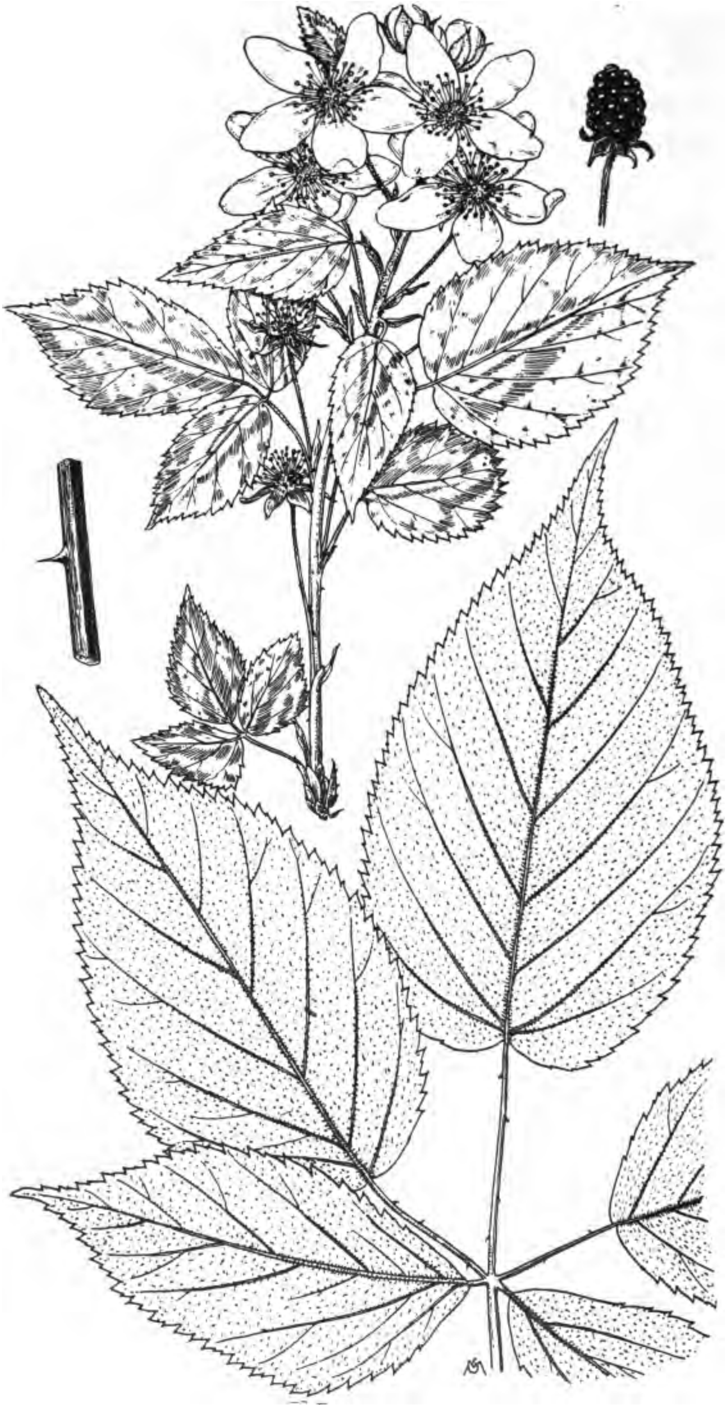


PLATE XI

R. pergratus Blanchard

Three-fifths natural size.

SHORT BLACKBERRY. SQUARE BLACKBERRY

Rubus pergratus Blanchard, Rhodora 8: 96. 1906

Stems ascending and recurving, furrowed, gland-tipped hairs and bristles absent; prickles 2-4 mm. long, broad-based and straightish, about 6 per dm. of cane; leaves on turions 5-foliolate, of early summer densely velvety beneath; terminal leaflet oval or oblong ovate; rhachis and pedicels densely villous, glandless; racemes short, 8-12-flowered; pedicels unarmed; fruit short cylindric and fleshy; seeds large, about 2½ mm. long.

Pollen about 70% imperfect. Seedlings do not segregate in culture.

Time of blooming: June 10 to July 18.

Time of fruiting: August 10 to September 12.

Type station: Alstead, New Hampshire.

Distribution: Thickets and woodland borders at medium altitudes throughout New England.

There are at present no cultivated varieties that are identical with this wild species, although its berries picked from the wild are often sold in the markets. By improvement, either by selection or by hybridization, it ought to produce a berry very desirable from the horticultural point of view.

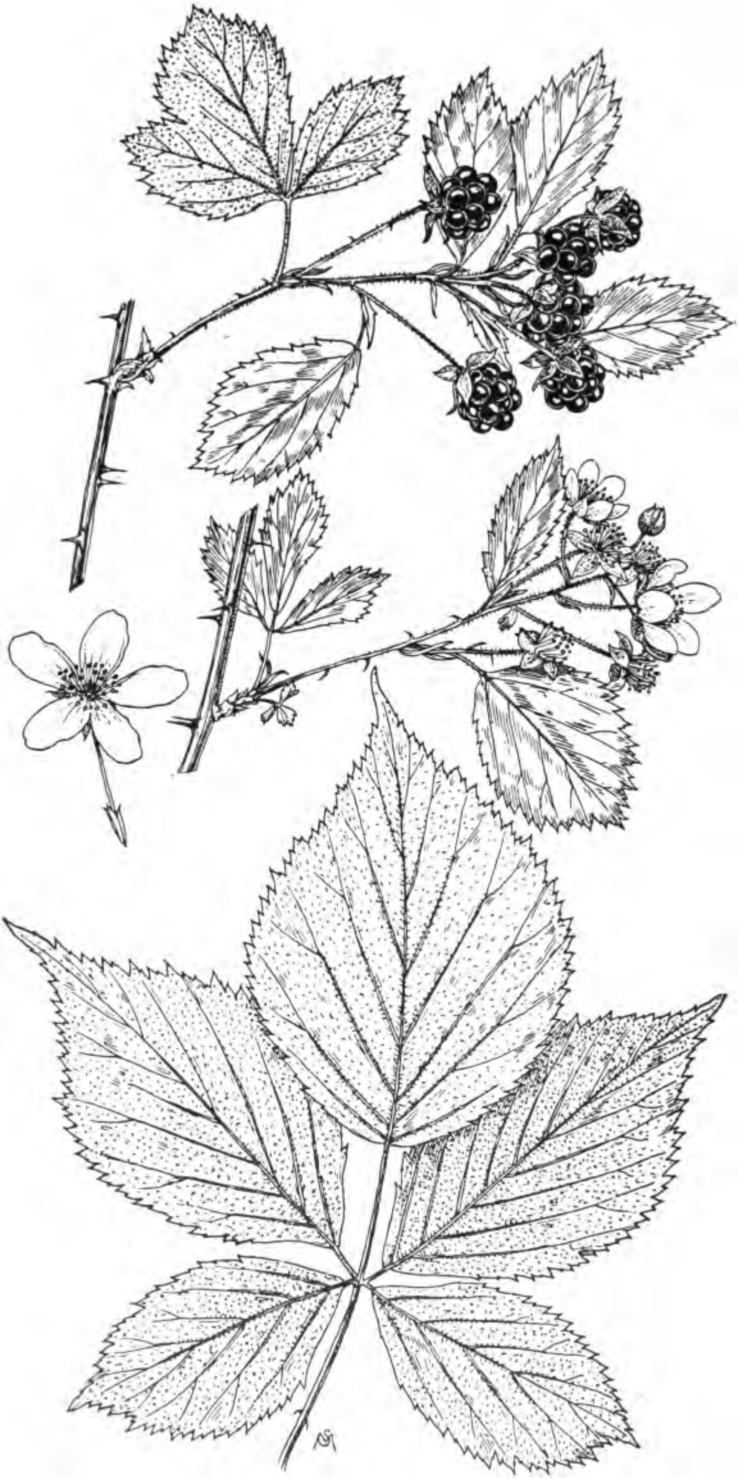


PLATE XII

R. frondosus Bigelow

Four-fifths natural size.

LEAFY-FLOWERED BLACKBERRY

Rubus frondosus Bigelow, Fl. Bost. Ed. 2: 199. 1824
Rubus recurvans Blanchard, Rhodora 6: 223. 1904
Rubus arundelanus Blanchard, Rhodora 8: 176. 1906
Rubus philadelphicus Blanchard, Torreya 7: 56. 1907
Rubus brainerdi Rydb., No. Am. Fl. 22: 467. 1. 1913

Stems arched recurving, nearly cylindrical, armed with stout, straight and somewhat recurved prickles, devoid of gland-tipped hairs and bristles; leaves on turions mostly 5-foliolate, of early summer subglabrous above, velvety beneath; the terminal leaflet suborbicular or broadly ovate; racemes 8-12-flowered, glandless; bracts of racemes more or less leafy; drupelets few, large, black, sweet and pulpy; seeds large, about 2½ mm. long.

Pollen about 75% imperfect. Seedlings grown from this species show quite a range of variation as to shape of leaves, serration of leaflets, etc., but not in respect to specific characters.

Time of blooming: June 5 to July 12.

Time of fruiting: July 20 to September 1.

Type station: Boston (Roxbury), Mass.

Distribution: Open fields and hillsides in southern New England. The form *R. recurvans* Blanchard extends further north into Maine, New Hampshire and Vermont.

As grown in the wild the plant is quite confusing to the systematist on account of its behavior under different environmental conditions. Its frondoseness is increased by light and drought and diminished by shade and moisture. Its erectness of growth is likewise effected by environment. A northern form, having narrower leaflets and fewer leafy bracts on racemes, is recognized.

From the horticultural standpoint, this blackberry is by far the most important of all our New England wild species and on account of its plasticity under cultural conditions it ought to be readily improved by plant breeders.

Closely related cultivated varieties are: Bangor, Joy, LaGrange, Ohmer, Sugar Plum, Tory, Ward and Watt. Its hybrids with *R. argutus* and *R. allegheniensis* are also cultivated.

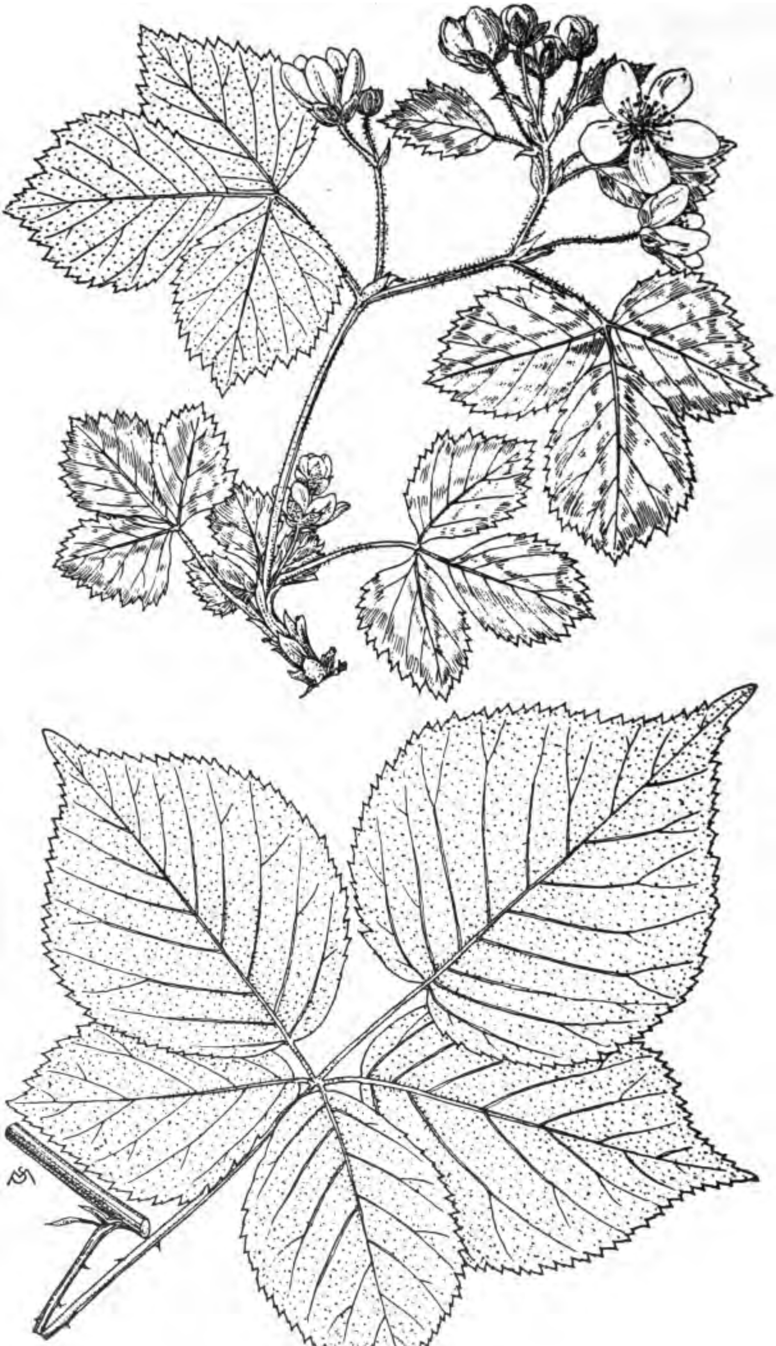


PLATE XIII

R. brainerdi Rydb.
Four-fifths natural size.

R. brainerdi Rydb. is a marked illustration of the confusion which has existed in the taxonomic literature of the American Rubi in the past. The type plant from Weybridge, Vt., was first determined by L. H. Bailey as "a small form of *R. nigrobaccus sativus*"—a name by which he designated an imagined wild progenitor of the short-cluster blackberries of cultivation. But based upon no definite type (14), Brainerd (13) in a discussion of the plant to which Bailey had applied this varietal name is accredited with the elevation of this variety to specific rank through a too liberal revision of his manuscript by the editors of Rhodora. Rydberg (3) in order to conform with the rules of priority renamed this hypothetical species and used the Weybridge plant as the type upon which it is based. The plant, however, sent Bailey is but a form of *R. frondosus* Bigelow as shown by a comparison of the plants under cultivation.

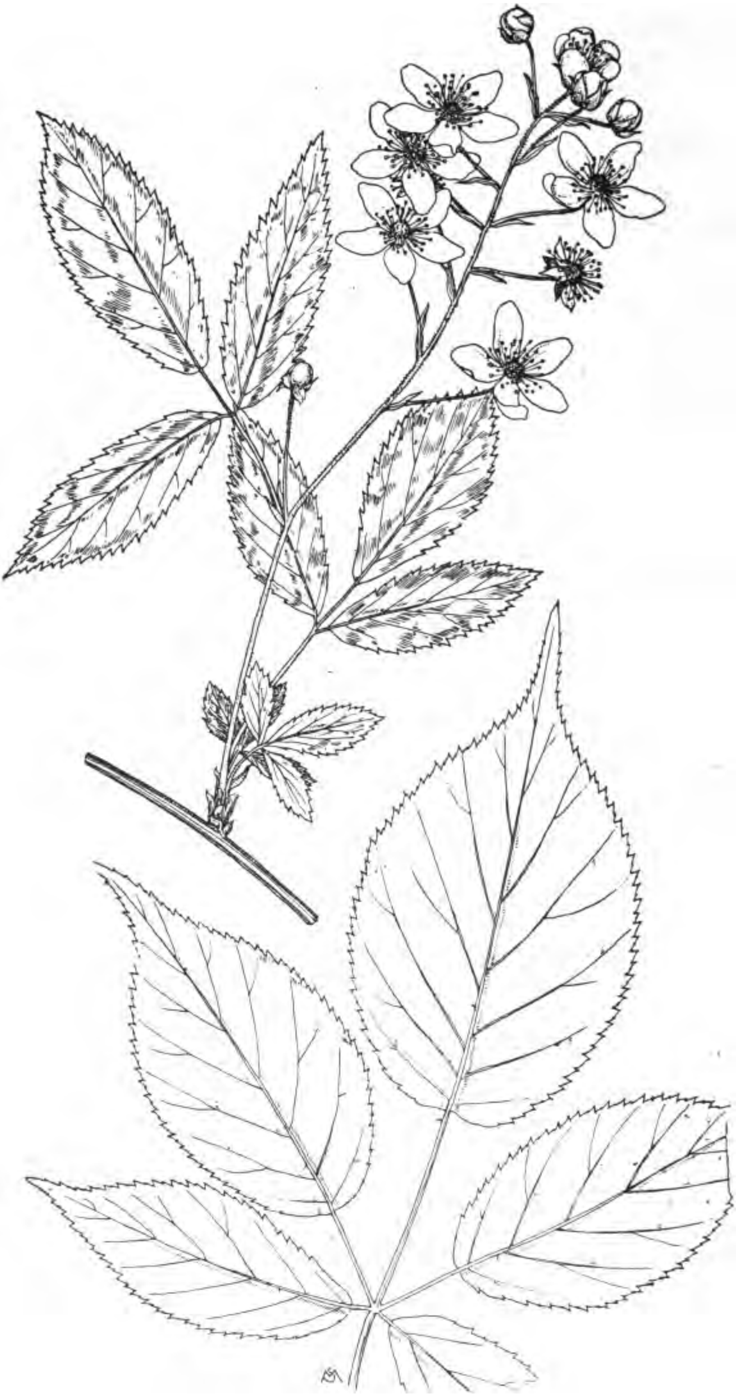


PLATE XIV

R. canadensis L.

Two-fifths natural size.

MOUNTAIN BLACKBERRY. THORNLESS BLACKBERRY

Rubus canadensis L. Sp. Pl. 494. 1753

Rubus randii (Bailey) Rydb., Britton Man. 497. 1901

Rubus millspaughii Britton, Bull. Torrey Club 18: 366. 1891. [See Ill. Fl. 2: 279]

Rubus amabilis Blanchard, Rhodora 8: 173. 1906. Not *R. amabilis* Focke. 1905

Rubus amicalis Blanchard, Rhodora 13: 56. 1911

Stems ascending and recurving, sometimes reddish or purplish, glabrous, unarmed or with few rudimentary prickles, gland-tipped hairs and bristles absent; leaves on turions mostly 5-foliolate; leaflets long-acuminate or acute, glabrous on both surfaces; inflorescence a loose cylindrical cymose-raceme, eglandular, tomentulose; drupelets large, juicy and somewhat acid.

Pollen about 85% imperfect. Seedlings do not show any segregation in culture.

Time of blooming: June 10 to July 16.

Time of fruiting: August 20 to September 25.

Type station: Canada.

Distribution: In thickets and along woody borders at higher altitudes throughout New England; sometimes descending into the lower valleys. It is the common blackberry of our mountain woodland.

"The Thornless Blackberry" is nothing but a cultivated form of this species.

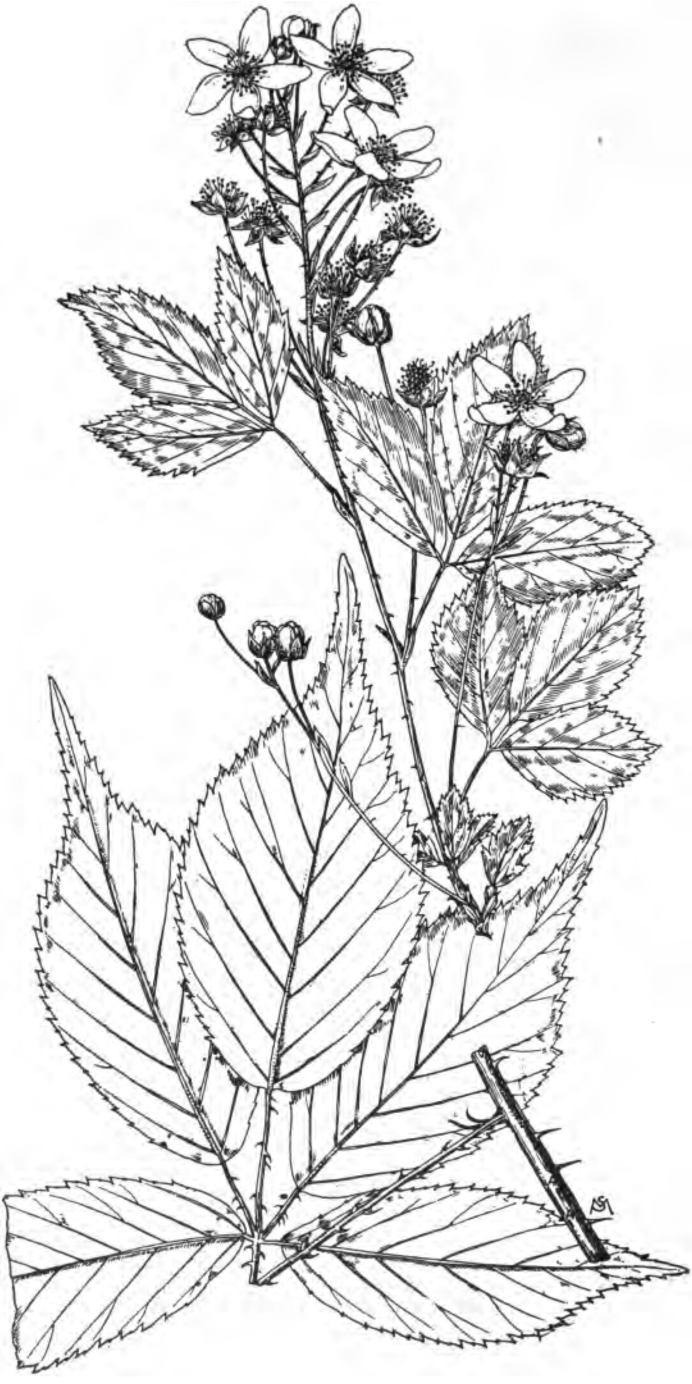


PLATE XV
R. elegantulus Blanchard
Two-thirds natural size.

SHOWY-FLOWERING BLACKBERRY
NEEDLE BLACKBERRY

Rubus elegantulus Blanchard, Rhodora 8: 95. 1906

Stems slender, erect, usually reddish, glabrous; plants eglandular throughout; prickles long, needle-like with a broad base, about 4 or 5 to the cm. of cane; leaves on turions mostly 5-foliolate, glabrous on both surfaces; petioles, petiolules and midveins armed with slender recurved prickles; racemes long, sometimes compound, with few short prickles; pedicels obscurely tomentulose; flowers large, showy; drupelets few, large; fruit globose, sweet.

Pollen about 70% imperfect. Seedlings do not seem to segregate in culture.

Time of blooming: June 10 to July 18.

Time of fruiting: August 20 to September 28.

Type stations: Stratton, Vt. and elsewhere.

Distribution: At high altitudes throughout Vermont and New Hampshire.

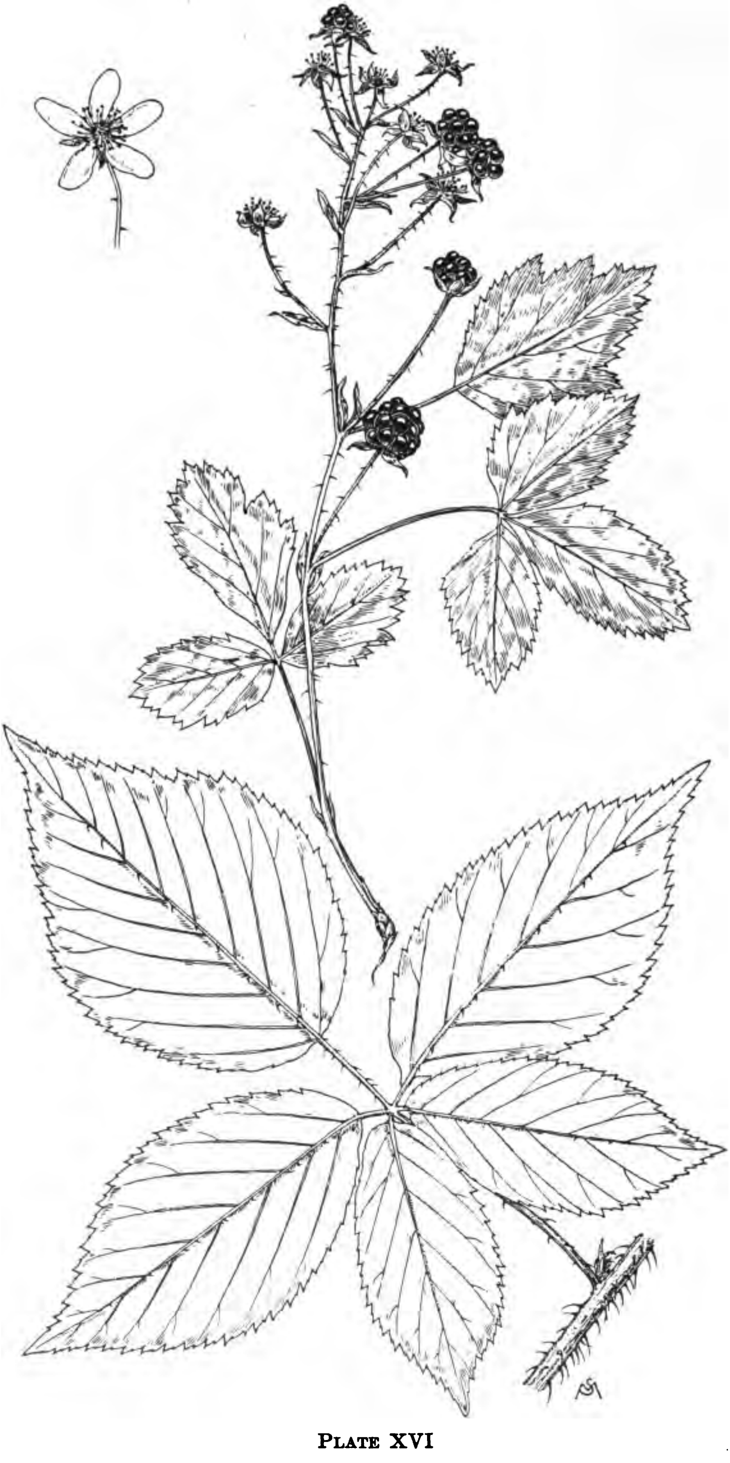


PLATE XVI

R. vermontanus Blanchard
Two-thirds natural size.

VERMONT BLACKBERRY

Rubus vermontanus Blanchard, Am. Bot. 7: 1. 1904

Rubus nigricans Rydb., Britton Man. 498. 1901 (in part). Not as amended in No. Am. Fl. 22: 476. 1913

Rubus peculiaris Blanchard, Rhodora 8: 174. 1906

Rubus nigricans Rydb., Gray Man. Ed. 7: 491. 1908 as to description.

Stems ascending and recurving, armed with numerous bristle-pointed prickles, about 20 to the cm. of cane; plants eglandular and glabrous throughout; leaves on turions mostly 5-foliolate, glabrous on both surfaces; terminal leaflet about twice as long as wide; cymose-racemes 6-12-flowered, 1-5 from the axil of each leaf; drupelets large, few; fruit globose.

Pollen about 85% imperfect. Seedlings do not segregate in culture.

Time of blooming: June 15 to July 22.

Time of fruiting: August 17 to September 12.

Type station: One and a half miles south of Windham, Vt.

Distributions: Frequent at about 1,000 feet altitude throughout Vermont and New Hampshire.

Although the fruit of this species is small, it is a profuse bearer. No varieties from this species are known to be cultivated for their fruit.

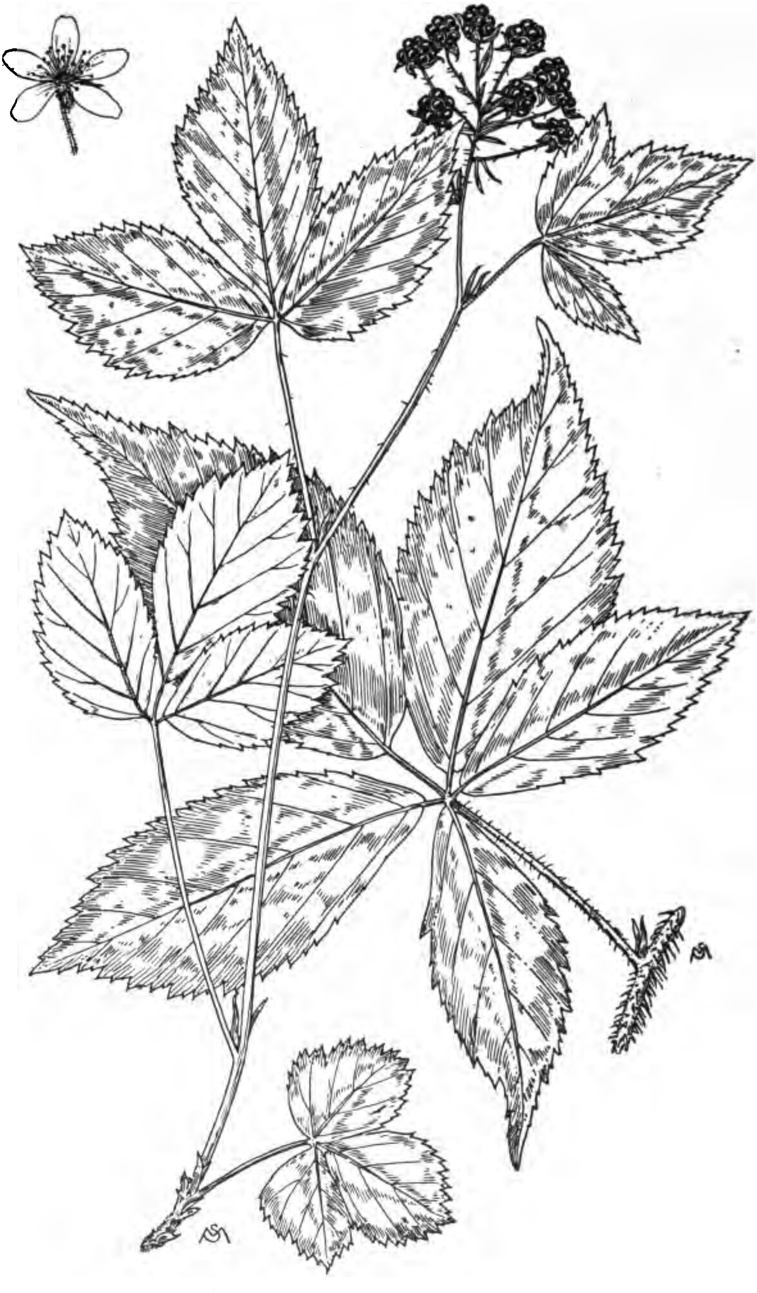


PLATE XVII

R. setosus Bigelow

Three-fourths natural size.

BRISTLY BLACKBERRY

Rubus setosus Bigelow, Fl. Bost. Ed. 2, 198. 1824. Gray Man. 491. 1908.

Rubus hispidus suberectus Peck, Ann. Rep. N. Y. State Mus. 44: 31. 1891. Not *R. suberectus* Anders. 1815

Rubus nigricans Rydb., Britton Man. 498. 1901 (in part). No. Am. Fl. 22: 476. 1913

Stems ascending and recurving, sometimes more or less prostrate, densely covered with retrose bristles, about 40 to the cm. of cane; gland-tipped bristles abundant on stem, petiole, raceme and calyx; leaves of turions mostly 5-foliolate, sometimes trifoliolate, glabrous on both surfaces; inflorescence a corybos cymose-raceme; fruit hemispherical, red; drupelets few.

Pollen about 80% imperfect. Seedlings do not show any segregation of specific characters when grown in culture.

Time of blooming: July 1 to August 1.

Time of fruiting: August 25 to September 22.

Type station: Sudbury, Mass.

Distribution: Throughout New England at high altitudes and in bogs and wet places at lower levels.

This species has very commonly been confused with *R. vermontanus* Blanchard although the two species are very distinct.

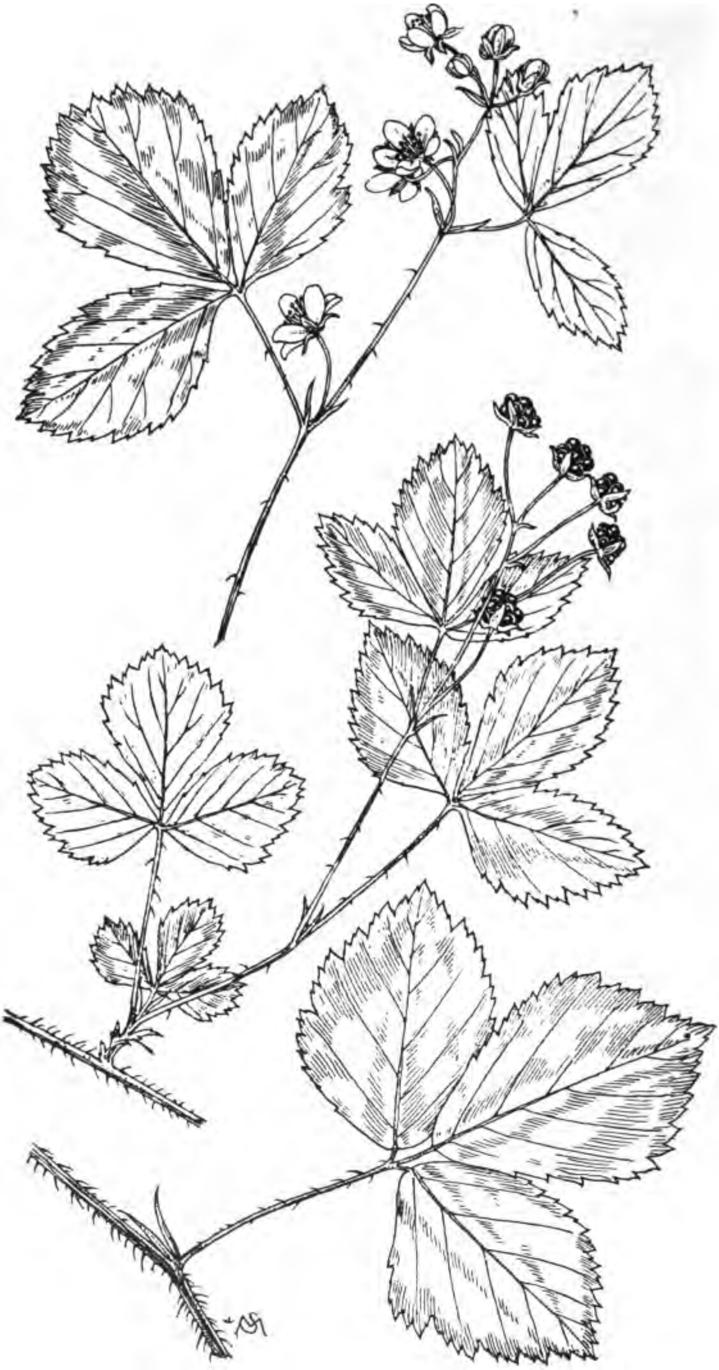


PLATE XVIII

R. hispidus L.

Natural size.

RUNNING SWAMP BLACKBERRY. HISPID BLACKBERRY

Rubus hispidus L. Sp. Pl. 493. 1753

Stems slender, terete, long and trailing, beset with many slender reflex bristles; leaves on turions mostly 3-foliolate; terminal leaflet obovate; leaflets glabrous on both surfaces, smooth, thickish, somewhat shiny above, mostly persistent during the winter; rhachis and pedicels often bristly and even glandular; inflorescence a few-flowered, close cymose-raceme; fruit of few drupelets, reddish-purple; drupelets small; sour.

Pollen about 90% imperfect. Seedlings show very little variation from parent plant.

Time of blooming: July 4 to July 31.

Time of fruiting: August 18 to September 20.

Type station: Canada.

Distribution: Low woods or swampy grounds throughout New England.

This is a unique and interesting species but of no horticultural importance, except in certain crosses with southern forms as *R. floridus* Tratt.

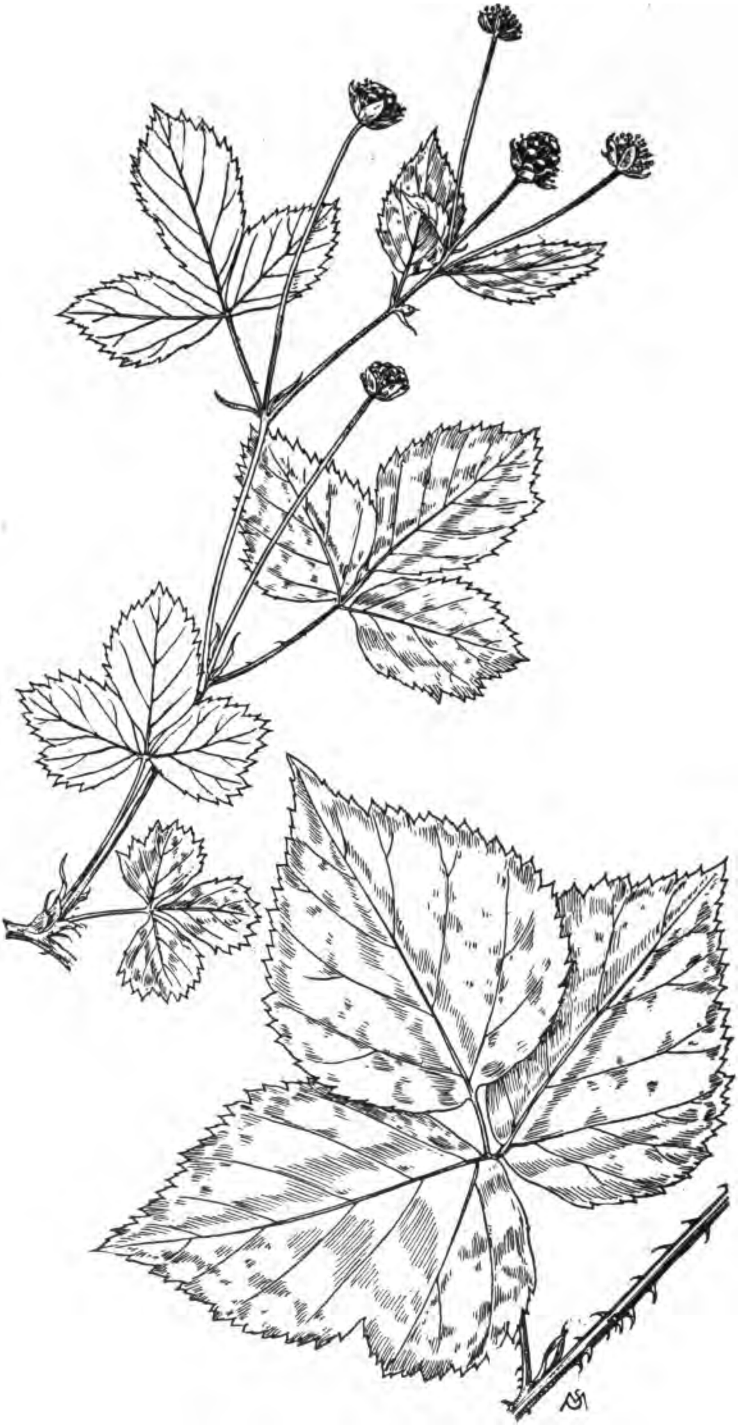


PLATE XIX

R. flagellaris Willd.

Four-fifths natural size.

WHIP BLACKBERRY

Rubus flagellaris Willd., Enum. 549. 1809
Rubus canadensis of Gray Man., Ed. 2. 1857. (Not *R. canadensis* L.)
Rubus procumbens Muhl., Muhl. Cat. 50. 1813

Stems terete, whip-like (often becoming thicker as it grows), trailing widely, often 3-4 meters long, armed with stiff hooked prickles 2-3 mm. long and about 2-5 to the cm. of cane; leaves on turions mostly 3-foliolate, sometimes 5-foliolate; leaflets somewhat sharply serrate, smooth above, slightly hairy beneath especially the veins; terminal leaflet on turions orbicular; pedicels erect, elongate, usually 2-5-flowered; fruit large, black, hemispheric; drupelets 15-30, large.

Pollen about 10% imperfect. Seedlings grown from this species show little or no variation from the parent plant.

Time of blooming: June 6 to July 1.

Time of fruiting: August 1 to September 10.

Type stations: North America.

Distributions: Dry ground in open fields and meadows throughout New England.

R. flagellaris Willd, has received quite different treatments by the various Eubatologists. Bailey (14) considers it a "puzzle" although he reproduces a very excellent photograph of the type specimen which he obtained at Berlin. In the latest editions of Gray's (2) and Britton's (1) manuals it is not even mentioned as a synonym while Rydberg (3) gives it specific rank. Focke in a discussion of the various doubtful forms of dewberries in his final work on *Rubus* asks the following question concerning it: *"Anne forma major robusta R. procumbentis?"* We are confident that what the American botanists have been naming *R. flagellaris* Willd. is nothing but a robust form of *R. procumbens* Muhl. Our cultivated plants of this species answer perfectly to Willdenow's description and his type specimen, which was a garden form, appears to be identical with our cultivated plants of *R. procumbens* Muhl, which have been collected from various parts of New England. We are therefore forced to accept Willdenow's name for our common northern dewberry as it antedates by four years even Muhlenberg's catalog name.

This plant does not seem to have entered very largely into our cultivated dewberries, as its berries are quite inferior to those of *R. baileyanus* Britton and *R. enslenii* Tratt.

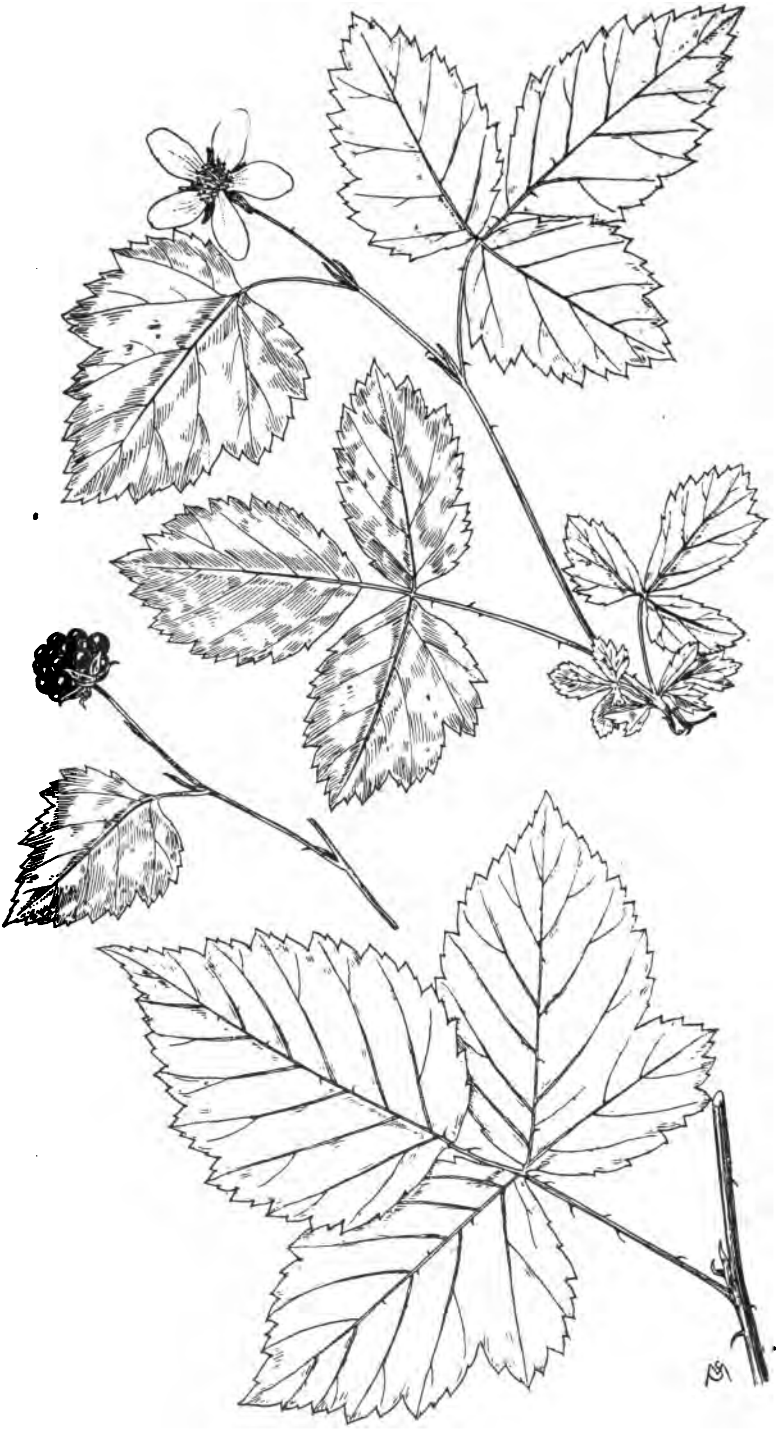


PLATE XX

R. enslenii Tratt.

Two-thirds natural size.

ENSLEN'S BLACKBERRY. DEWBERRY

Rubus enslenii Tratt. Ros. Monog. 3: 63. 1823

Stems terete, slender, trailing, glabrous, sparingly armed with small hooked prickles about 1-2 to the cm. of cane; leaves on turions mostly 3-foliolate; leaflets double-serrate with broadly rounded mucronate teeth, glabrous on both surfaces, ciliolate; flowers mostly solitary; pedicels glandless; fruit large, black, few drupelets.

Pollen about 10% imperfect.

Time of blooming: June 3 to July 1.

Time of fruiting: August 2 to September 1.

Type stations: North America.

Distributions: Open fields and meadows in southern New England, and southward.

Some of the cultivated forms of this species are Chestnut and Eight Ells. Illinois is undoubtedly a cross between this species and *R. frondosus* Bigelow.

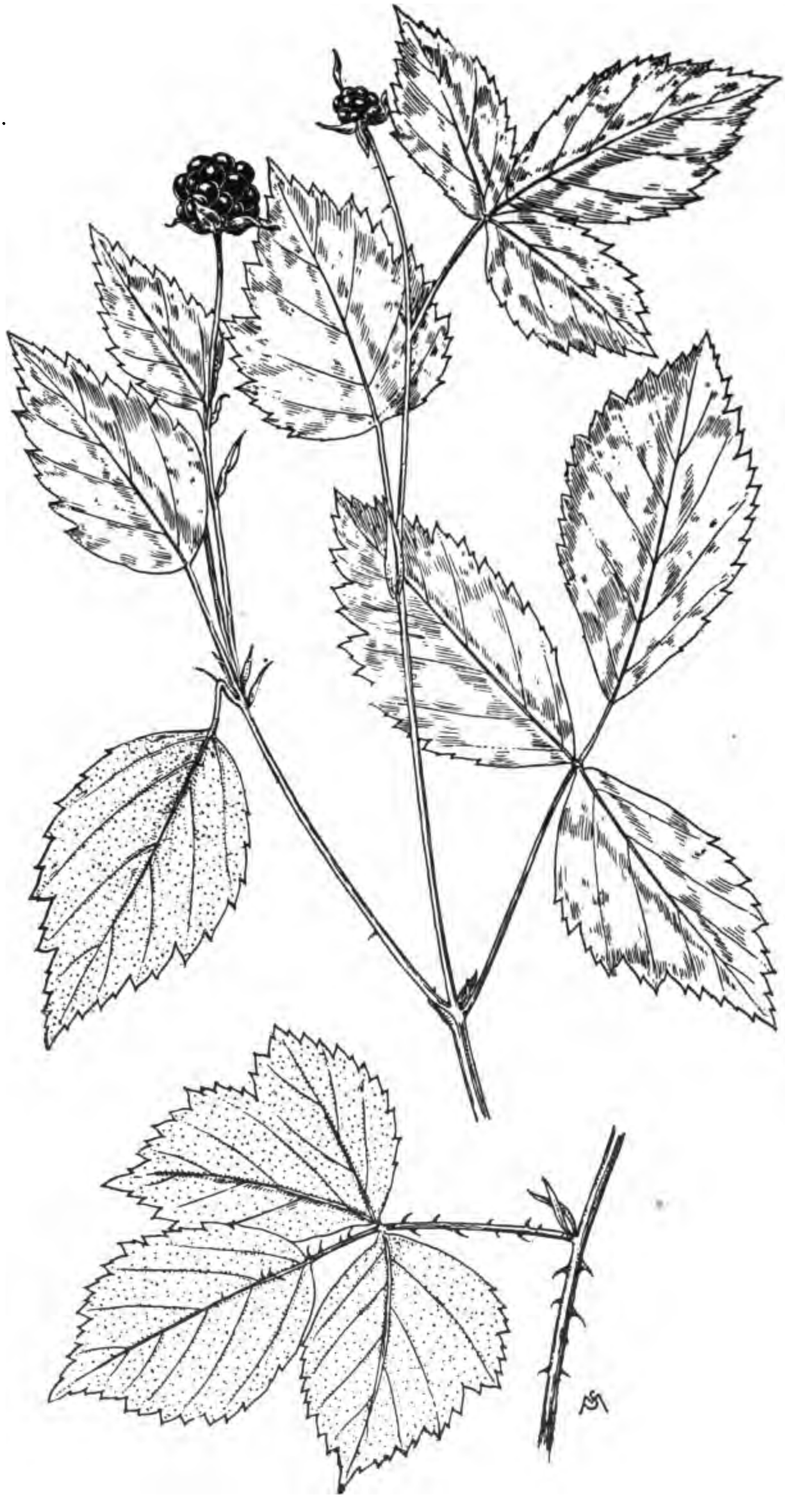


Plate XXI

R. baileyanus Britton

Four-fifths natural size. An eglandular form.

BAILEY'S BLACKBERRY. DEWBERRY

Rubus baileyanus Britton, Mem. Torrey Club 5: 185. 1894

Rubus villosus humifusus T. & G., No. Am. Fl. 1: 455. 1840. Not *R. humifusus* Weihe. 1825.

Rubus invisus Britton, Bull. Torrey Club 20: 279. 1893. Not *R. canadensis invisus* Bailey. 1891.

Stems terete, trailing, often beset with stalked or sessile glands, sparingly armed with stiff hooked prickles 2-3 mm. long and about 1-3 to the cm. of cane; leaves on turions mostly 3-foliolate; terminal leaflet ovate; leaflets with course broadly rounded mucronate teeth, of early summer pubescent beneath; pedicels erect, elongate, often glandular, usually 1-3-flowered; flowers somewhat large; fruit black, few drupelets; seeds large.

Pollen about 10% imperfect. Seedlings grown from this plant show very little variation.

Time of blooming: May 26 to June 30.

Time of fruiting: July 31 to August 30.

Type station: West Point, N. Y.

Distribution: Dry fields, along fence-rows and open woods throughout New England, except in the extreme north.

The characters of this species are very prominent in a large number of our common cultivated dewberries. From this species have been developed, either directly or indirectly through hybridization, some of our most prized dewberries of cultivation. The probable origin of some of these is indicated as follows: Rathbun, Thompson's Early Mammoth—*R. argutus X baileyanus;* Crandall, Robinson—*R. baileyanus X betulifolius;* Bartel, General Grant, Mammoth, Premo—*R. baileyanus X enslenii;* Austin's, Cox Lucetia—*R. baileyanus X floridus.*

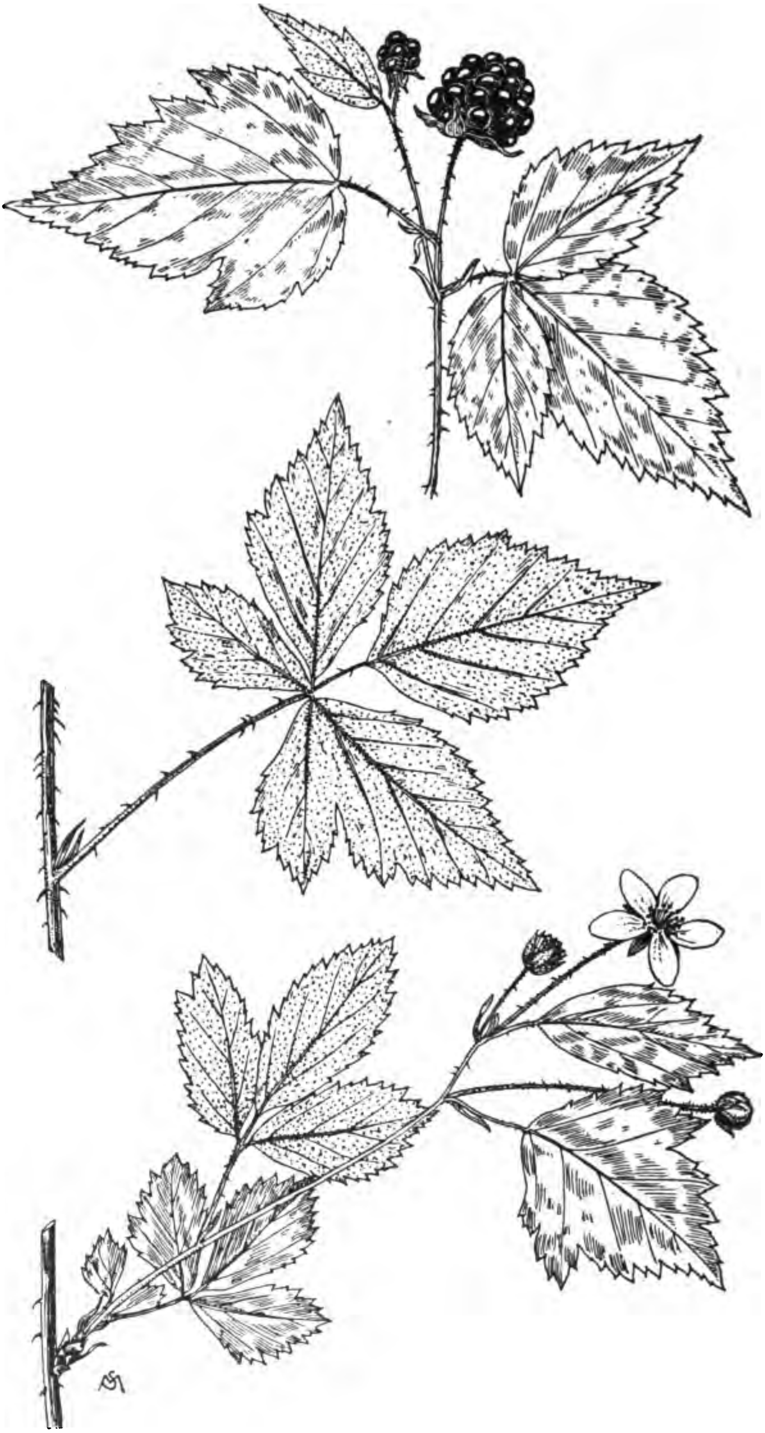


PLATE XXII

R. baileyanus Britton

Four-fifths natural size. A glandular form.

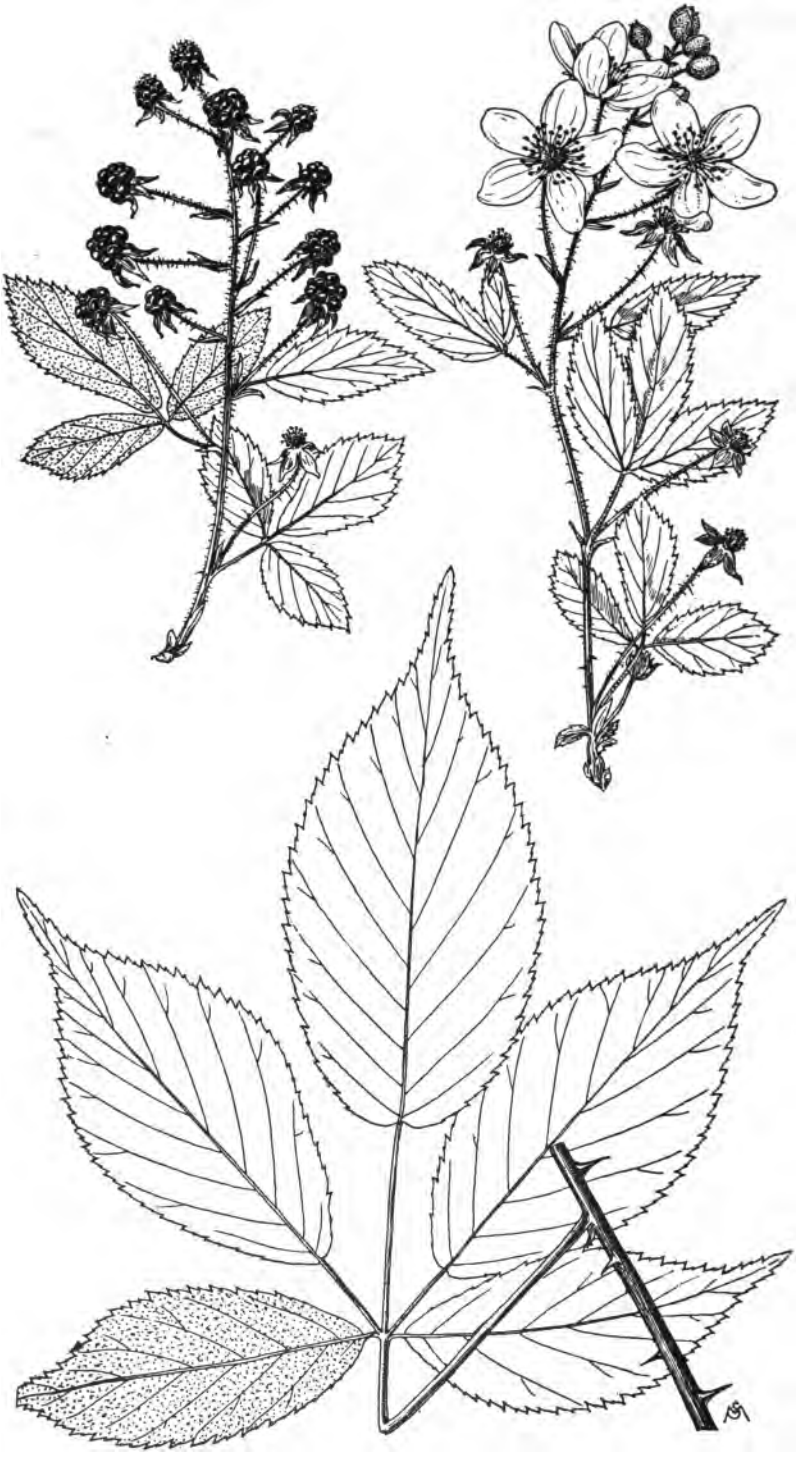


PLATE XXIII

R. alleghenlensis X argutus

Two-thirds natural size.

RUBUS ALLEGHENIENSIS X ARGUTUS

Rubus andrewsianus Blanchard, Rhodora 8: 17. 1906
Rubus alleghenienis X *argutus* Bicknell, Bull. Torrey Club 38: 111. 1911

Stems erect, armed with strong, straight, broad-based prickles, mostly glabrous with a few scattered gland-tipped hairs; leaves on turions mostly 5-foliolate, of early summer somewhat pubescent on the lower surface; terminal leaflet oval or obovate; inflorescence bearing gland-tipped hairs; pedicels armed with hooked prickles; seeds large.

Resembles *R. argutus* in having prickles on pedicels, almost glabrous new canes and large seeds; resembles *R. allegheniensis* in having pubescent leaves and glandular inflorescence; the shape of the leaflets, the number of flowers in the raceme and the size and shape of prickles are intermediate.

Pollen about 80% imperfect. Numerous plants grown from the seeds of this hybrid vary towards both parent species.

Collected at the following stations: Weybridge, Vt.; Southington, Conn. (type station); Hague, N. Y.; Milton, Mass.; North Hanover, Mass.; South Duxbury, Mass.; Manomet, Mass.; Indiana (C. C. Deam).

This hybrid is the probable progenitor of the following cultivated varieties: Ancient Britton, Badger, Dorchester, Eldorado, Lovett and Taylor.

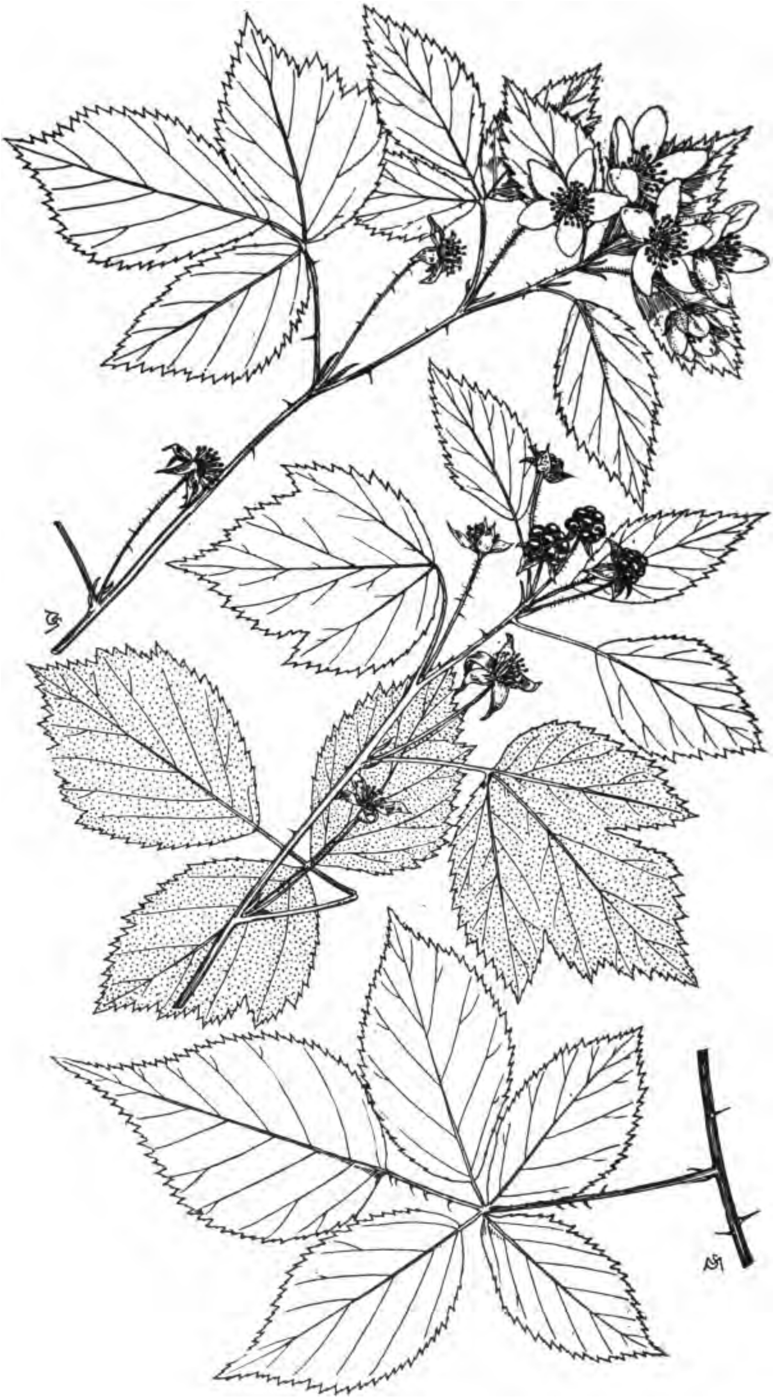


PLATE XXIV

R. argutus X frondosus

Two-thirds natural size.

RUBUS ARGUTUS X FRONDOSUS

Rubus jeckylanus Blanchard, Rhodora 8: 177. 1906*

Rubus argutus X *frondosus* Bicknell, Bull. Torrey Club 38: 114. 1911

Stems ascending and recurving, glabrous and glandless, armed with strong, slightly hooked prickles; leaves on turions mostly 5-foliolate, of early summer velvety beneath; the terminal leaflet broadly ovate, petioles and petiolules armed with hooked prickles; racemes leafy-bracted, cymose-corymbose; pedicels armed and often having a few scattered glands; fruit ovoid.

Resembles *R. argutus* in having leafy-bracted inflorescence and broadly ovate leaflets; other characters are intermediate.

Pollen about 60% imperfect.

Collected at Kennebunkport, Me. (type station); also at Brookline, Mass. and from garden at Middlebury, Vt.

This hybrid is the probable progenitor of the following cultivated varieties: Blowers, Erie, Jordan, Kittatinny, Mersereau, Minnewaski and Western Triumph.

---

*Named after a fictitious person who lived a double life in a well-known story of Stevenson. The flowering plant is attractive when seen, but atrocious when handled.

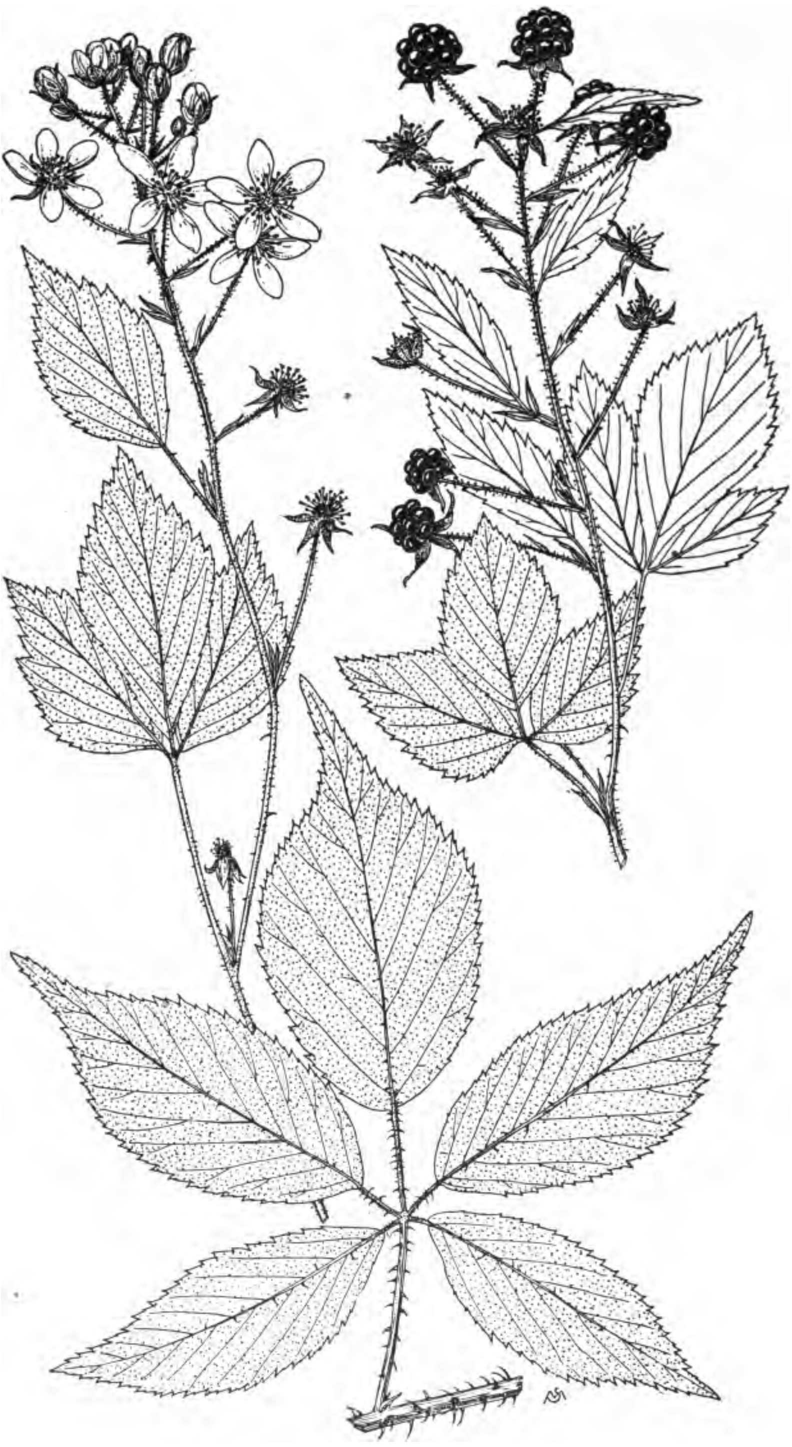


PLATE XXV

R. allegheniensis X elegantulus

Two-thirds natural size.

RUBUS ALLEGHENIENSIS X ELEGANTULUS

Rubus flavinanus Blanchard, Am. Bot. 10: 69. 1906

Stems ascending and recurving, glabrous and bearing a few gland-tipped hairs, armed with slender, hooked prickles with a broad, flattened base; leaves on turions mostly 5-foliolate, of early summer pubescent beneath; terminal leaflet on new canes obovate; petioles glandless, copiously armed with hooked prickles; racemes elongate; petals 1½ cm. long; pedicels very glandular; fruit globose, sweet.

Resembles *R. allegheniensis* in having glands on new canes and inflorescence and somewhat pubescent leaves; resembles *R. elegantulus* in having long, slender prickles, large, showy flowers and sweet, globose fruit; the shape of leaves, number of flowers in racemes and most of the other characters are intermediate.

Pollen about 65% imperfect. Seedlings from this plant vary towards the two parents.

Blanchard describes this plant as a dwarf form solely on account of the condition under which his type specimen grew. Plants from the type station which were transplanted to the plant breeding gardens of the station have developed into large, robust plants.

Collected at the type station, Stratton, Vt.

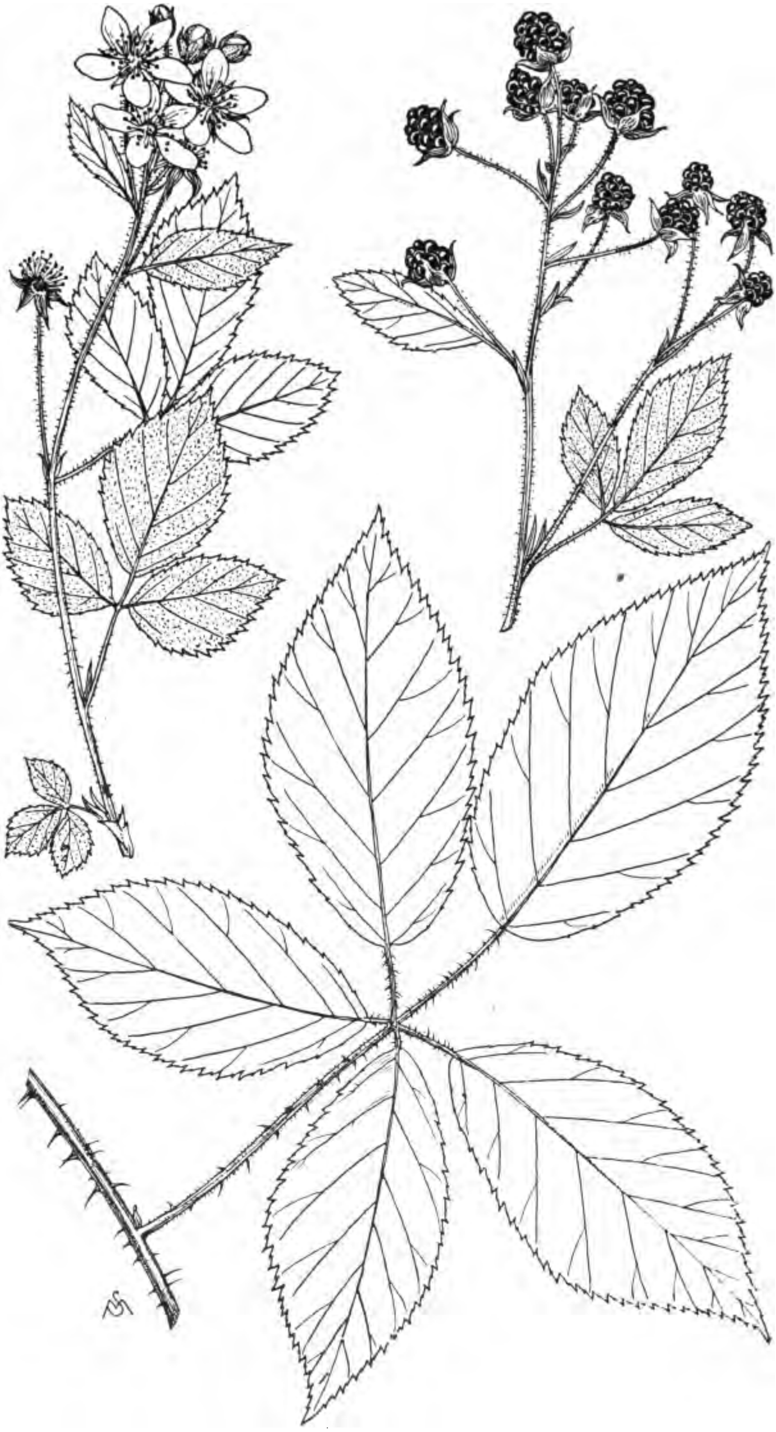


PLATE XXVI

R. allegheniensis X vermontanus

Four-fifths natural size.

RUBUS ALLEGHENIENSIS X VERMONTANUS

Rubus fraternus, hyb. nov.

Stems ascending and recurving, glabrous and bearing a few gland-tipped hairs, armed with long, slender prickles; leaves on turions mostly 5-foliolate, of early summer pubescent beneath; terminal leaflet on new cane oval or obovate; petioles glandless; often pubescent, armed with hooked prickles; racemes short; pedicels glandular, unarmed; flowers small.

Resembles *R. allegheniensis* in having glands on stems and inflorescence and in having pubescent leaves; resembles *R. vermontanus* in having short, broad racemes and globose fruit; the shape of leaf, number and size of prickles and number of flowers in racemes are intermediate.

Pollen about 60% imperfect.

Collected at the following stations: Stratton, Vt., north of old church (type station); Stratford, N. H. (Fernald).

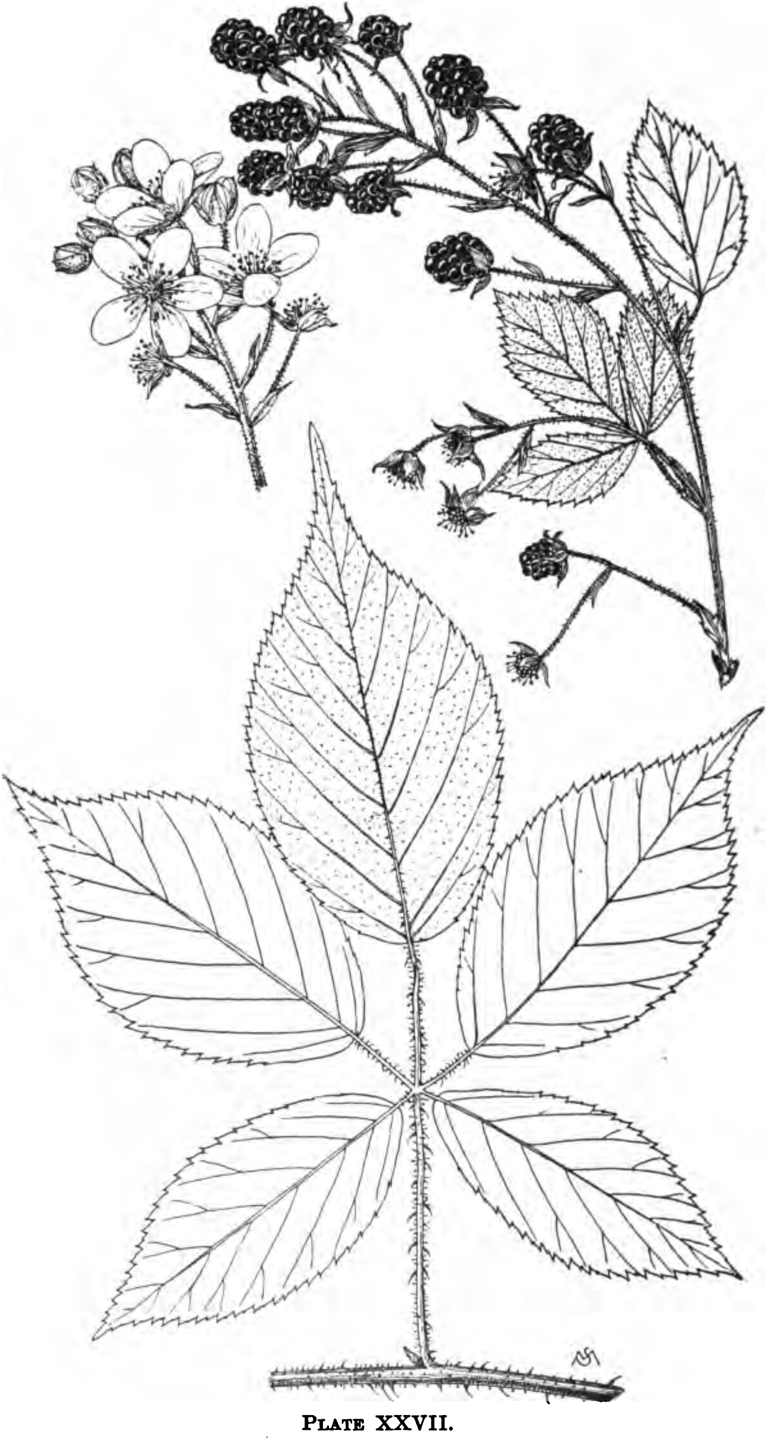


PLATE XXVII.

R. allegheniensis X setosus

Two-thirds natural size.

RUBUS ALLEGHENIENSIS X SETOSUS

Rubus glandicaulis Blanchard, Rhodora 8: 172. 1906

Stems erect and recurving, armed with strong prickles of varying sizes; stems, petioles, petiolules and inflorescence copiously beset with gland-tipped hairs and bristles; leaves on turions mostly 5-foliolate, of early summer velvety beneath; terminal leaflet oval; racemes elongate, 14-18-flowered; pedicels unarmed, often branched; drupelets large.

Resembles *R. pergratus* in having pubescent leaves and racemes and somewhat broad terminal leaflets; resembles *R. setosus* in having glandular stem and inflorescence; the number and size of prickles, shape of raceme and the number of flowers in racemes are intermediate.

Pollen about 60% imperfect.

Collected at the following stations: Kennebunk, Me. (Blanchard's type station); Eden, Vt.; Stewartstown, N. H. (Fernald).

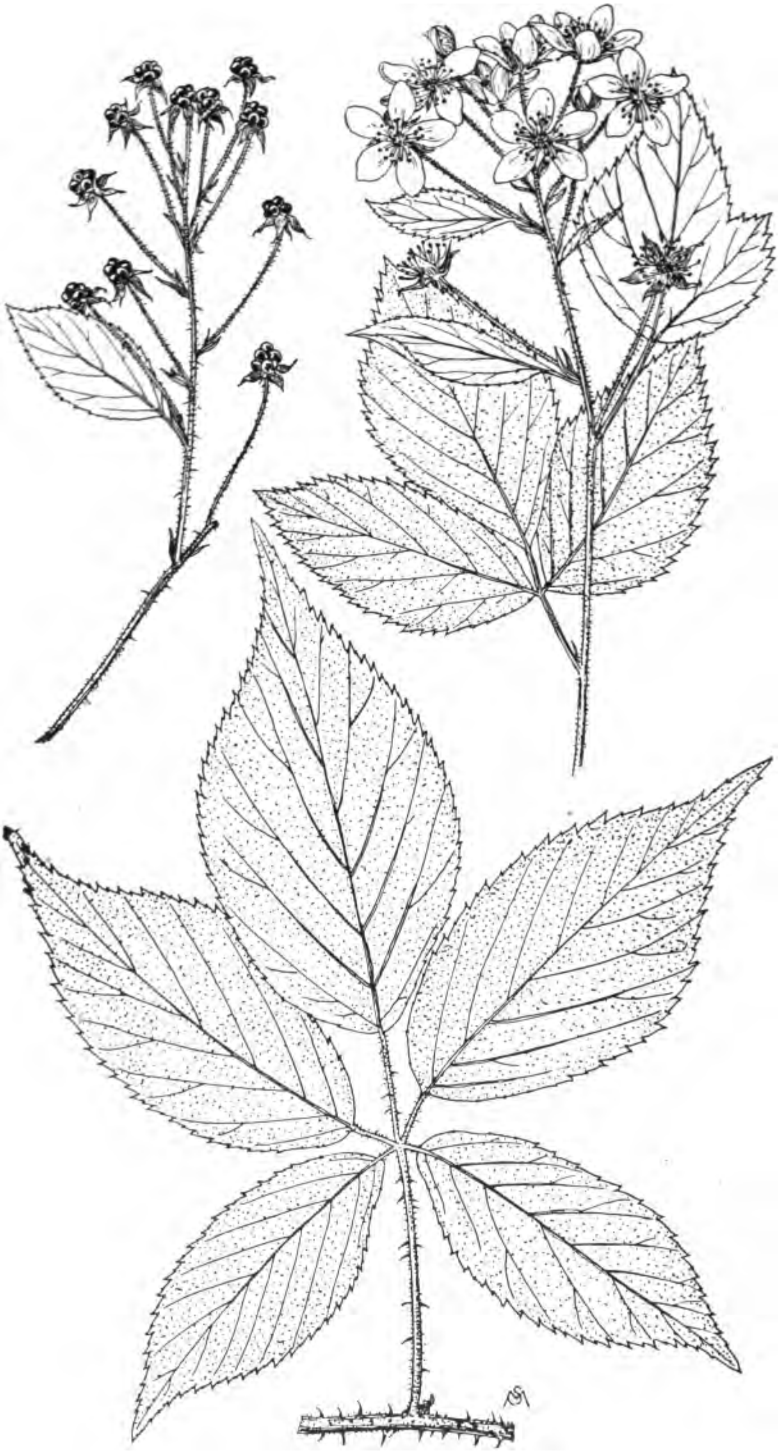


PLATE XXVIII

R. pergratus X setosus

Four-fifths natural size.

RUBUS PERGRATUS X SETOSUS

Rubus frondisentis Blanchard, Torreya 6: 119. 1906

Stems erect and recurving, armed with weak prickles of varying sizes; stems, petioles, petiolules and inflorescence copiously beset with gland-tipped hairs; leaves on turions mostly 5-foliolate, of early summer velvety beneath; terminal leaflet oval; racemes short, 8-11-flowered, very pubescent; pedicels unarmed; flowers often nearly sterile; seeds large.

Resembles *R. allegheniensis* in having pubescent leaves and inflorescence and a many-flowered raceme; resembles *R. setosus* in having bristles on the stem and inflorescence; the number and size of prickles, the size and shape of leaf and the shape and size of fruit are intermediate.

Pollen about 10% imperfect. Seedlings from this plant are very uniform and seem to breed true to the type.

Collected at the following stations: Townshend, Vt. (type station); Berkshire, Vt.; Stratton, Vt.; Stratford, N. H. (Fernald); Colebrook, N. H. (Fernald); Northumberland, N. H. (Fernald); Stewartstown, N. H. (Fernald).

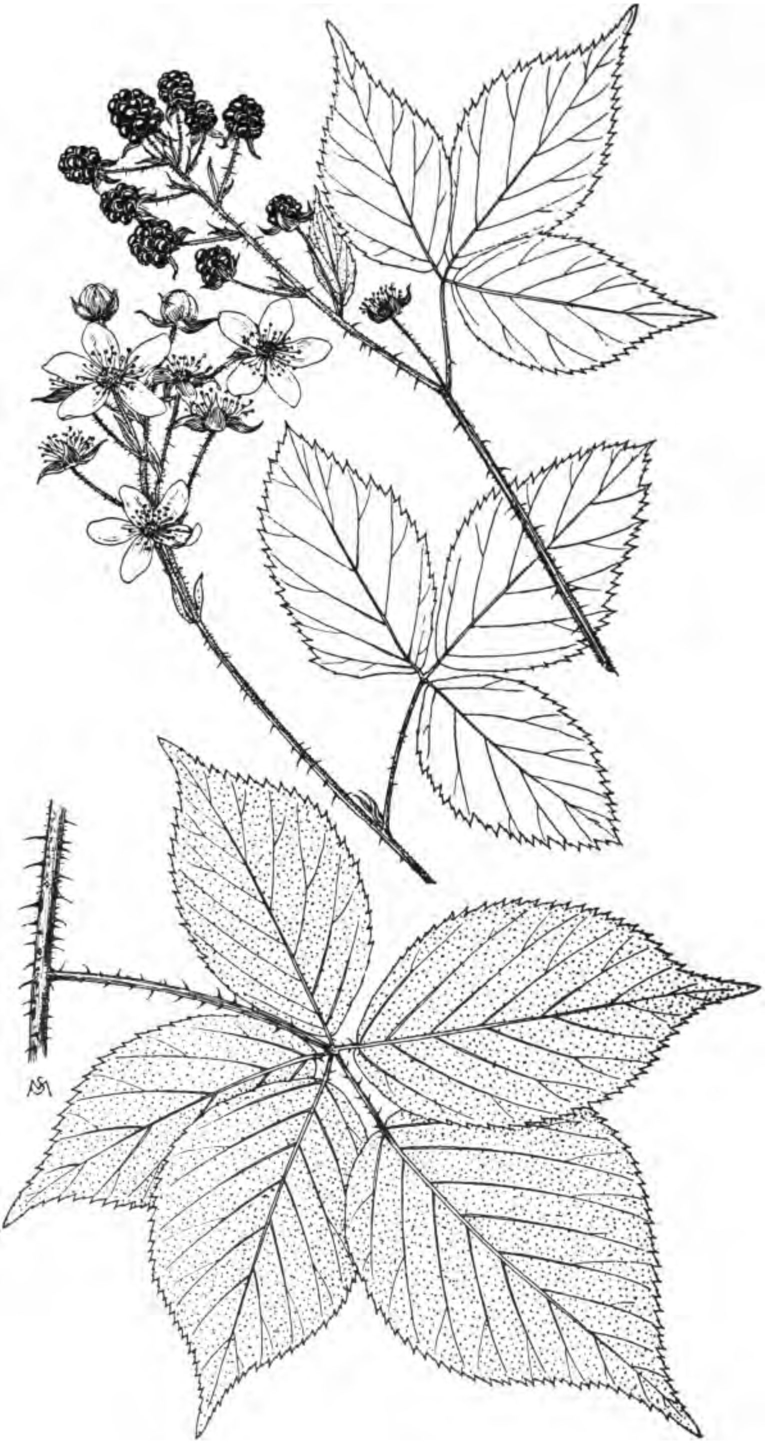


PLATE XXIX

R. frondosus X setosus

Two-thirds natural size.

R. FRONDOSUS X SETOSUS

Rubus abbrevians Blanchard, Torreya 6: 235. · 1906

Stems ascending and recurving, terete, glabrous, armed with numerous weak prickles of varying lengths; new canes and inflorescence glandular; leaves on turions mostly 5-foliolate, of early summer pubescent beneath; leaflets broadly ovate, lower leaflets nearly sessile; racemes short, 8-12-flowered; pedicels copiously beset with gland-tipped hairs and bristles; drupelets large; fruit globose.

Resembles *R. frondosus* in having broadly ovate and pubescent leaflets; resembles *R. setosus* in having stems and inflorescence glandular and setaceous prickles; other characters are more or less intermediate.

Pollen about 10% imperfect. Seedlings grown from the seeds of selfed flowers of this plant vary very little from the mother plant.

Collected at the following stations: Stevens's Hill, North Windham, Vt. (type station); Stratton, Vt.; West Dummerston, Vt.; Townshend, Vt.; Stratford, N. H. (Fernald); North Woodstock, N. H. (Fernald); Thornton, N. H. (Fernald).

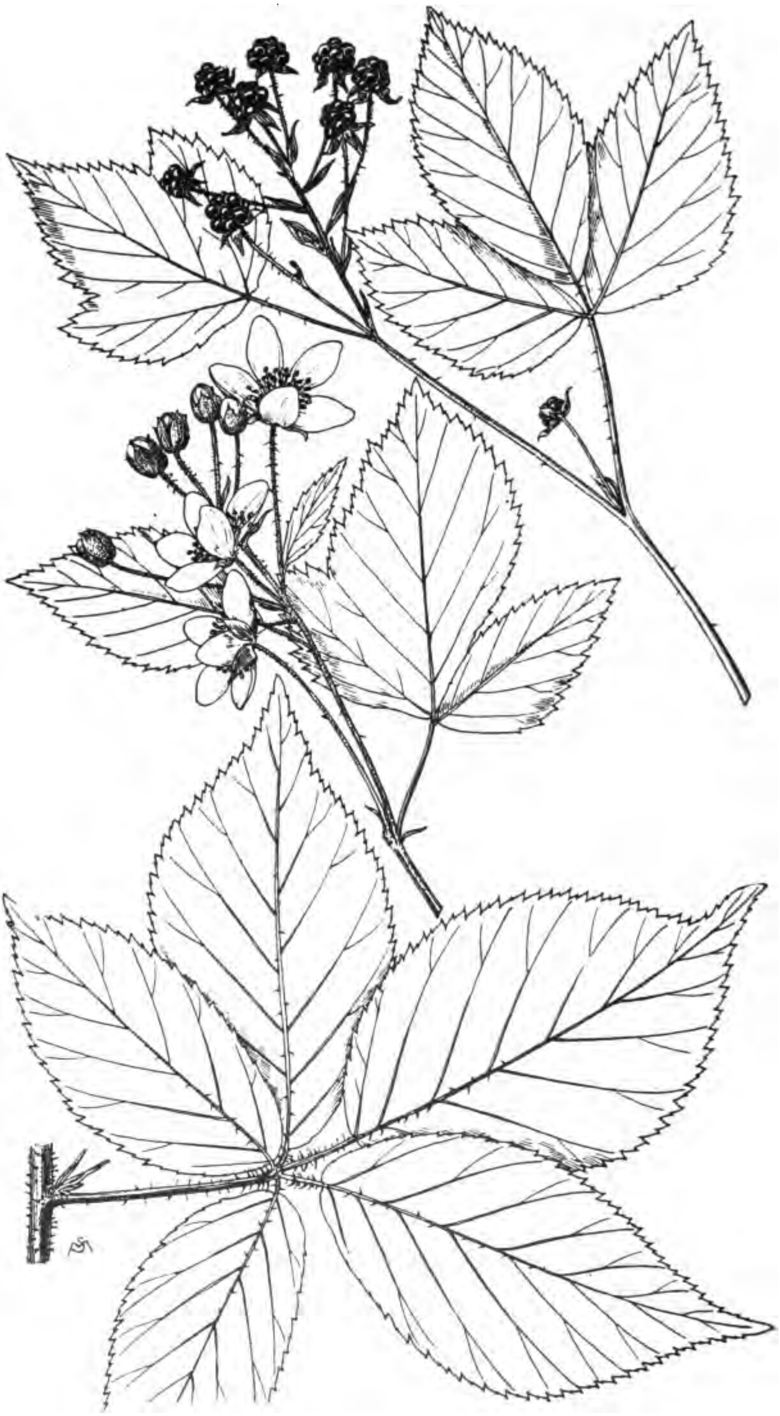


PLATE XXX

R. canadensis X setosus

Two-thirds natural size

RUBUS CANADENSIS X SETOSUS

Rubus junceus Blanchard, Rhodora 8: 215. 1906

Stems weak, erect and recurving, becoming more or less prostrate with age, armed with weak, setaceous prickles grading into bristles and gland-tipped hairs; leaves on turions mostly 5-foliolate, glabrous on both surfaces, terminal leaflet oval, lower leaflets nearly sessile; petiole and petiolules armed and glandular; rhachis villous and somewhat glandular; racemes short; pedicels 2-5 cm. long; fruit globose.

Resembles *R. canadensis* in having a villous rachis and oval leaflet; resembles *R. setosus* in having glands and setaceous prickles on cane, petioles and inflorescence and weak canes; the shape of raceme, size of flowers and other characters are intermediate.

Pollen about 85% imperfect.

Collected at the following stations: Kennebunk, Me. (type station); Stratton, Vt.; South Wardsboro, Vt.; West Wardsboro, Vt.; Wallingford, Vt.; North Woodstock, N. H.; Plymouth, N. H. (Fernald); Errol, N. H. (Fernald); Lincoln, N. H. (Fernald); Gorham, N. H. (Fernald); Woodstock, N. H. (Fernald); Thornton, N. H. (Fernald); Laconia, N. H. (Fernald); Gilford, N. H. (Fernald).

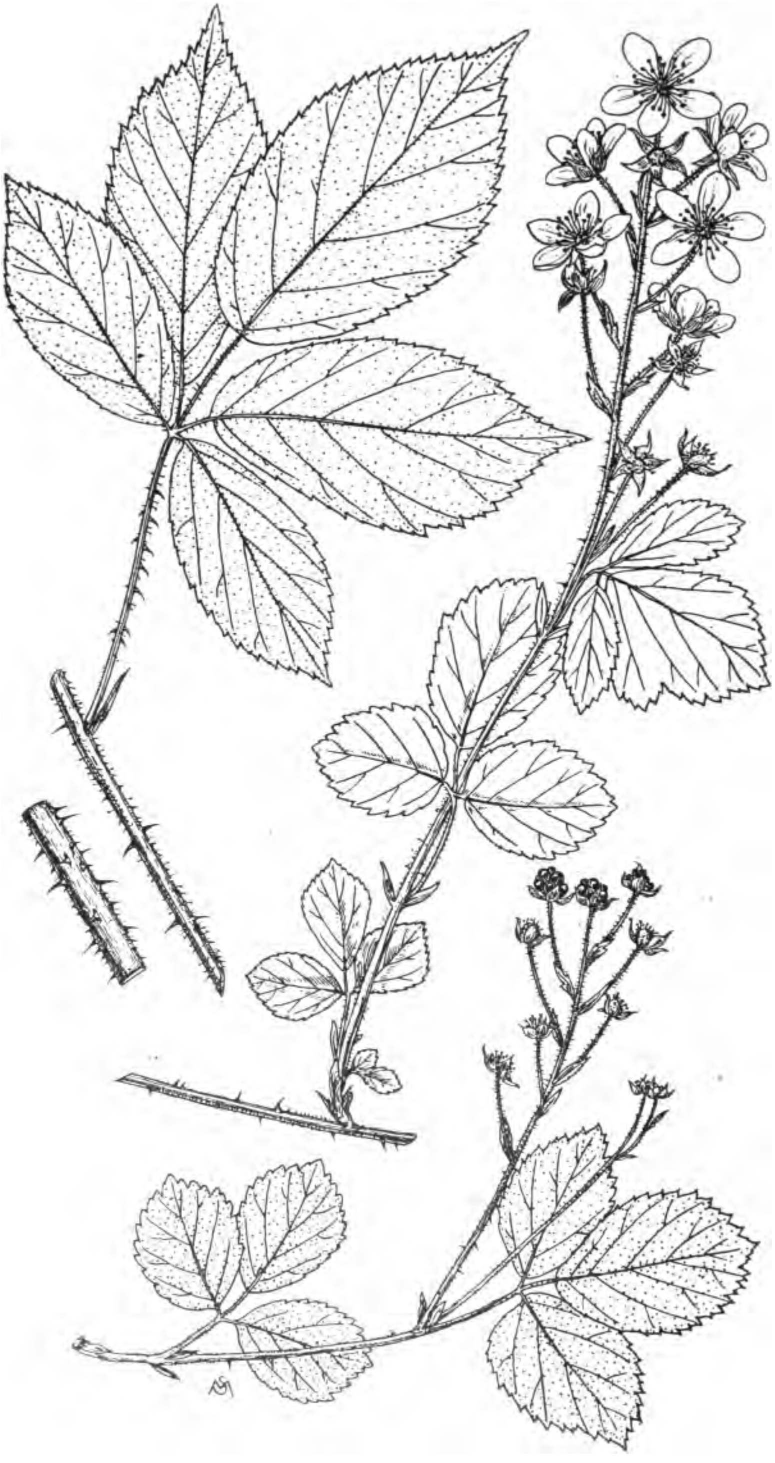


PLATE XXXI

R. allegheniensis X hispidus

Four-fifths natural size.

RUBUS ALLEGHENIENSIS X HISPIDUS

Rubus permixtus Blanchard, Torreya 6: 117. 1906

Stems recurving and soon prostrate, armed with numerous straightish prickles of unequal lengths; cane, petioles, petiolules and racemes beset with gland-tipped hairs and bristles grading into prickles; leaves on turions mostly 5-foliolate, of early summer velvety beneath; terminal leaflet about twice as long as wide; racemes 8-16-flowered, elongate, not leafy-bracted; fruit black.

Resembles *R. allegheniensis* in having mostly 5-foliolate leaves on turions, pubescent leaves, glandular cane and inflorescence, straightish prickles and black fruit; resembles *R. hispidus* in having trailing stems beset with bristles; the shape of raceme, number of flowers in racemes, shape of leaflets and other characters are more or less intermediate.

Pollen about 50% imperfect. Seedlings grown from the seed of this hybrid when selfed do not revert to the parent types.

Collected at the following stations: Westminster, Vt. (type station); Putney, Vt.; Burlington, Vt.; Walpole, N. H.; Burlington Co., N. J. (Darrow); Cambridge, N. Y. (Brainerd).

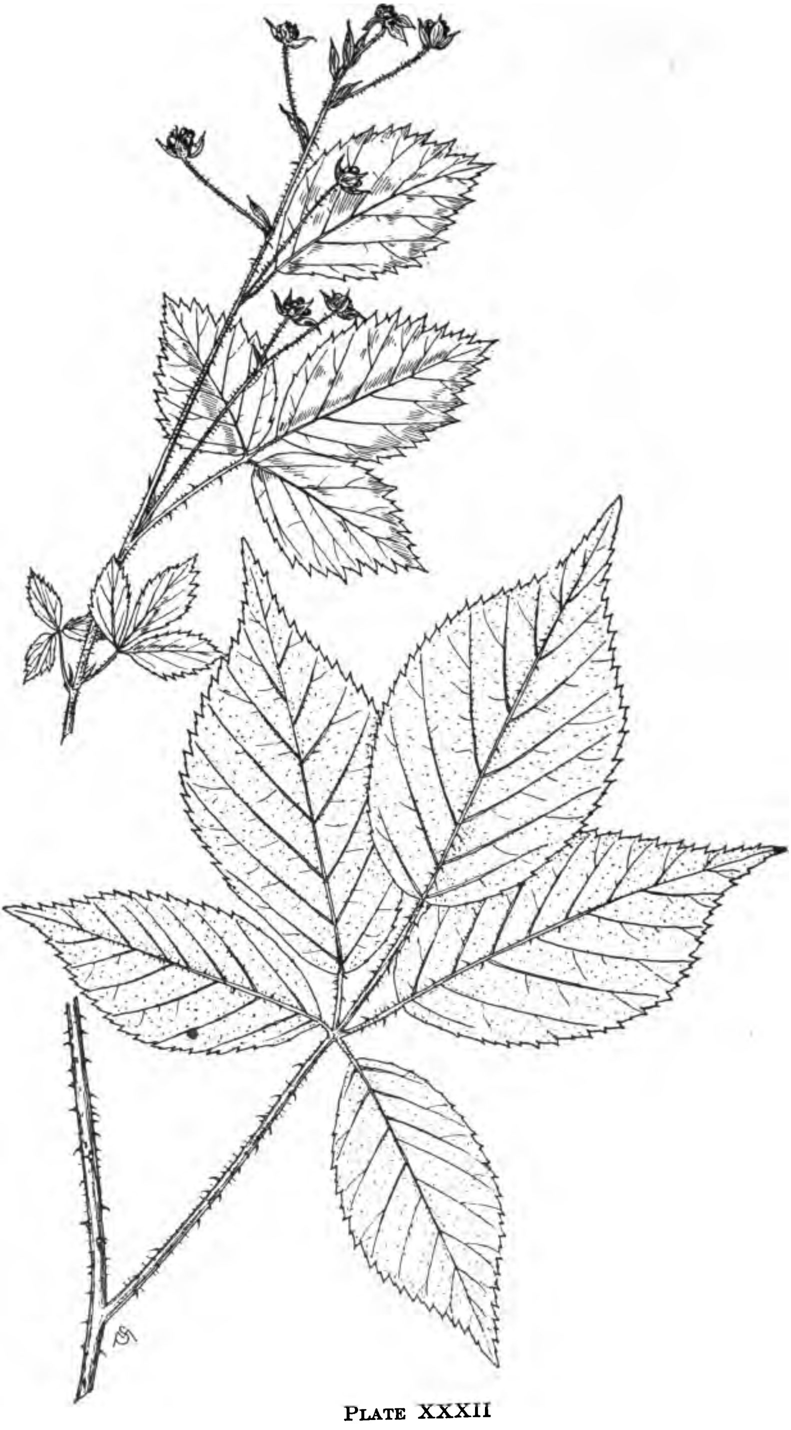


PLATE XXXII

R. allegheniensis X flagellaris

Eight-elevenths natural size.

RUBUS ALLEGHENIENSIS X FLAGELLARIS

Rubus elongatus, hyb. nov.

Stems prostrate, young shoots somewhat ascending, armed with hooked prickles, beset with gland-tipped hairs of uniform length; leaves on turions mostly 5-foliolate, of early summer velvety beneath; petiole and petiolules armed and glandular; terminal leaflet about twice as long as wide; inflorescence glandular; racemes 6-10-flowered; fruit small.

Resembles *R. allegheniensis* in having glandular cane and inflorescence and 5-foliolate leaves on turions; resembles *R. flagellaris* in having hooked prickles and prostrate stems; the amount of pubescence on leaves, shape of leaflets, shape of racemes and number of flowers in racemes are intermediate.

Pollen about 75% imperfect.

Collected at Cambridge, N. Y. (type station).

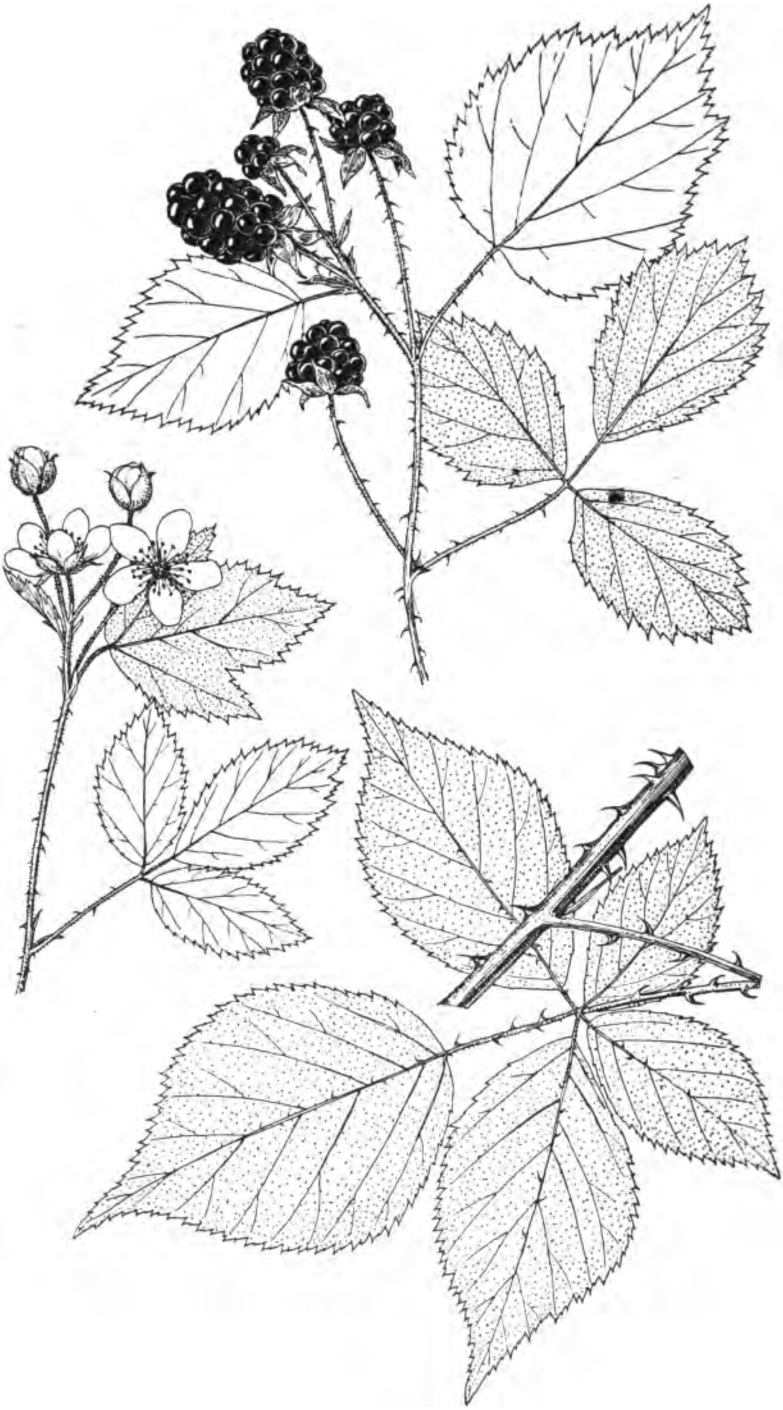


PLATE XXXIII

R. argutus X flagellaris

Two-thirds natural size.

RUBUS ARGUTUS X FLAGELLARIS

Rubus multispinus Blanchard, Torreya *7*: *7*. 1907

Stems recurving and soon becoming prostrate, armed with large, hooked prickles, about 5 to the cm. of cane; cane leaves and inflorescence glandless; leaves on turions mostly 5-foliolate, often 3-foliolate, of early summer somewhat pubescent beneath; terminal leaflet broadly ovate; racemes few-flowered, corymbose; pedicels pubescent, armed with hooked prickles; fruit large, short, cylindrical, black.

Resembles *R. argutus* in having mostly 5-foliolate leaves on turions, armed pedicels and pubescent leaves; resembles *R. flagellaris* in having procumbent stems and broadly ovate leaflets on new canes; the shape of raceme, number of flowers in racemes and the shape and size of fruit are intermediate. The prickles are larger than those of either of the parent plants but have the shape of those of *R. flagellaris*.

Pollen about 65% imperfect.

Collected at the following stations: Rocky Point, R. I. (type station); Rehoboth, Mass.; South Duxbury, Mass.; Michigan City, Ind. (Deam).

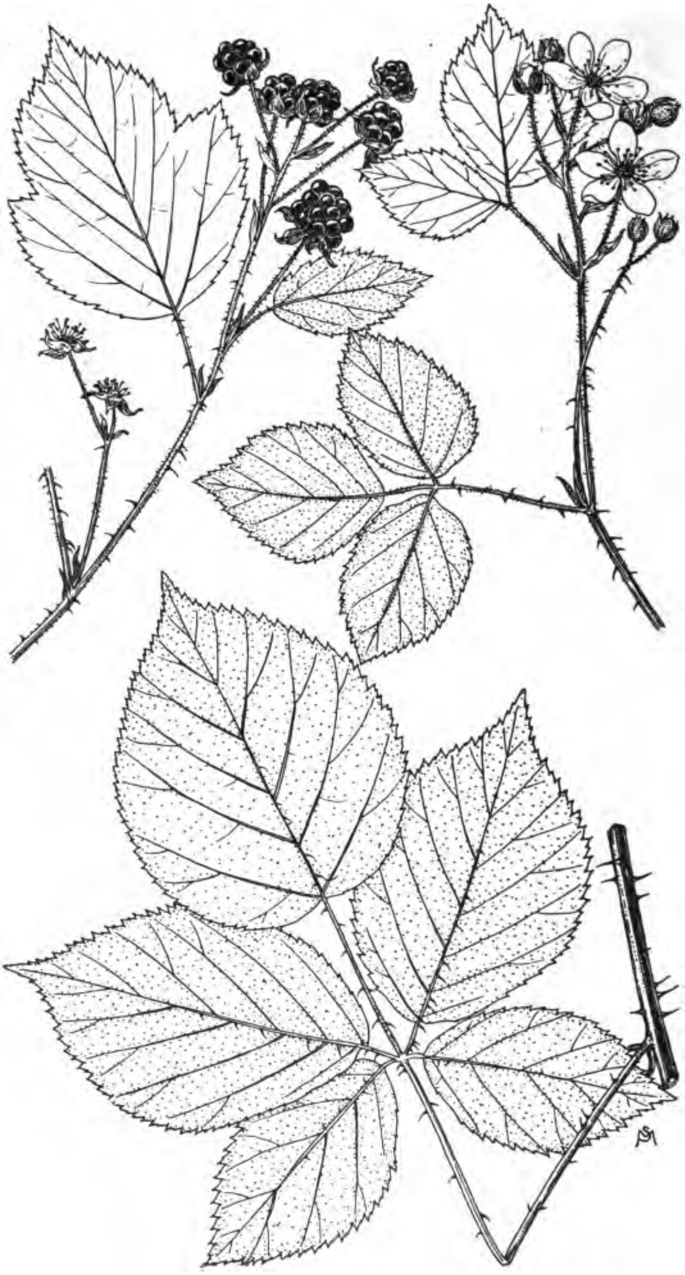


PLATE XXXIV

R. baileyanus X frondosus

Seven-elevenths natural size.

RUBUS BAILEYANUS X FRONDOSUS

Rubus arenicola Blanchard, Rhodora, 8: 170. 1906

Stems recurving and soon becoming prostrate, glabrous, armed with straightish prickles about 5 mm. long; leaves on turions mostly 5-foliolate, often 3-foliolate, of early summer pubescent beneath; terminal leaflet orbicular; inflorescence corymbose, 4-8-flowered, lower flowers leafy-bracted; pedicels pubescent and glandular; fruit large, globose, black.

Resembles *R. baileyanus* in having prostrate stems and somewhat glandular inflorescence; resembles *R. frondosus* in having on turions 5-foliolate leaves, straightish prickles and orbicular terminal leaflets; the number of prickles on stem, the amount of pubescence on leaves and inflorescence, number of flowers in raceme, size and shape of fruit and most other characters are intermediate.

Pollen about 80% imperfect.

Collected at the following stations: Kennebunk, Me. (type station); Plymouth, Mass.; Natick, Mass. (Darrow).

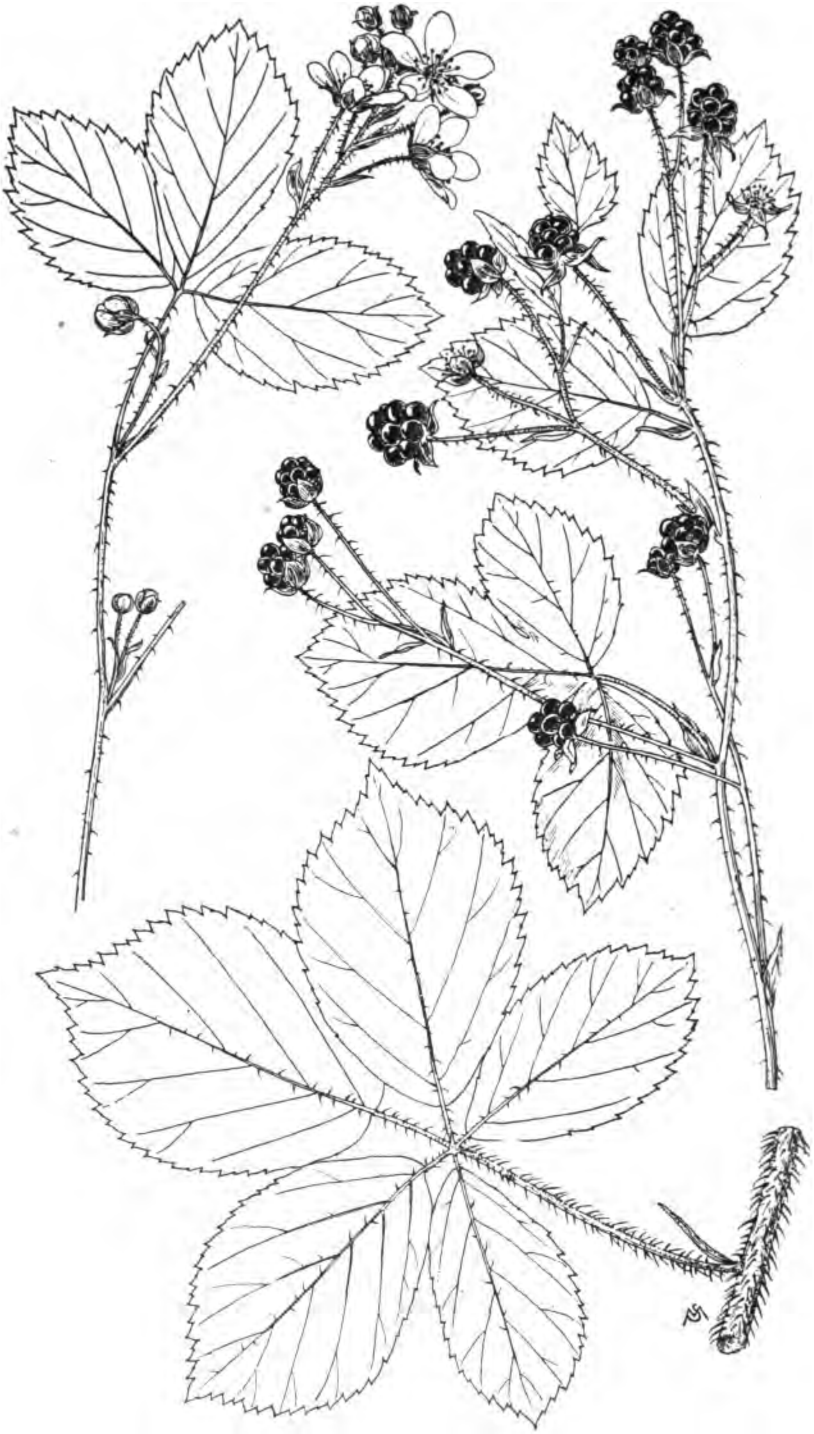


PLATE XXXV

R. hispidus X setosus

Four-fifths natural size.

RUBUS HISPIDUS X SETOSUS

Rubus jacens Blanchard, Torreya 6: 147. July, 1906
Rubus trifrons Blanchard, Am. Bot. 11: 11. Sept., 1906

Stems prostrate, terete, beset with numerous bristles grading into gland-tipped hairs, simple hairs absent; leaves on turions 5-foliolate, in some plants 3-foliolate, glabrous on both surfaces, frequently persistent through the winter; petioles, petiolules and midveins beset with bristles and gland-tipped hairs; terminal leaflet on turions obovate; inflorescence a cymose-raceme, often branched; pedicels slender, glandular, sparsely beset with weak bristles; flowers small; fruit globose; drupelets few, large; seeds large.

Resembles *R. hispidus* in having prostrate stems; resembles *R. setosus* in having sometimes 5-foliolate leaves on turions; the number and shape of bristles, number of gland-tipped hairs, shape of inflorescence, shape of terminal leaflet on turions and most other characters are intermediate.

Pollen about 85% imperfect. Numerous seedlings have been grown from both the 3-foliolate and the 5-foliolate type of this hybrid and in all cases they resemble in most respects one of the parent species.

Collected at the following stations: Alstead, N. H. (Blanchard's type station for *R. jacens;* West Wardsboro, Vt. (Blanchard's type station for *R. trifrons*) ; Stratton, Vt.; Townshend, Vt.; Westminster, Vt.; Marlboro, Vt.; Burlington, Vt.; Berkshire, Vt.; Ripton, Vt.; Troy, N. H.; Woodstock, N. H. (Fernald) ; Thornton, N. H. (Fernald) ; Lincoln, N. H. (Fernald) ; Gorham, N. H. (Fernald) ; Gilford, N. H. (Fernald) ; Lancaster, N. H. (Fernald).

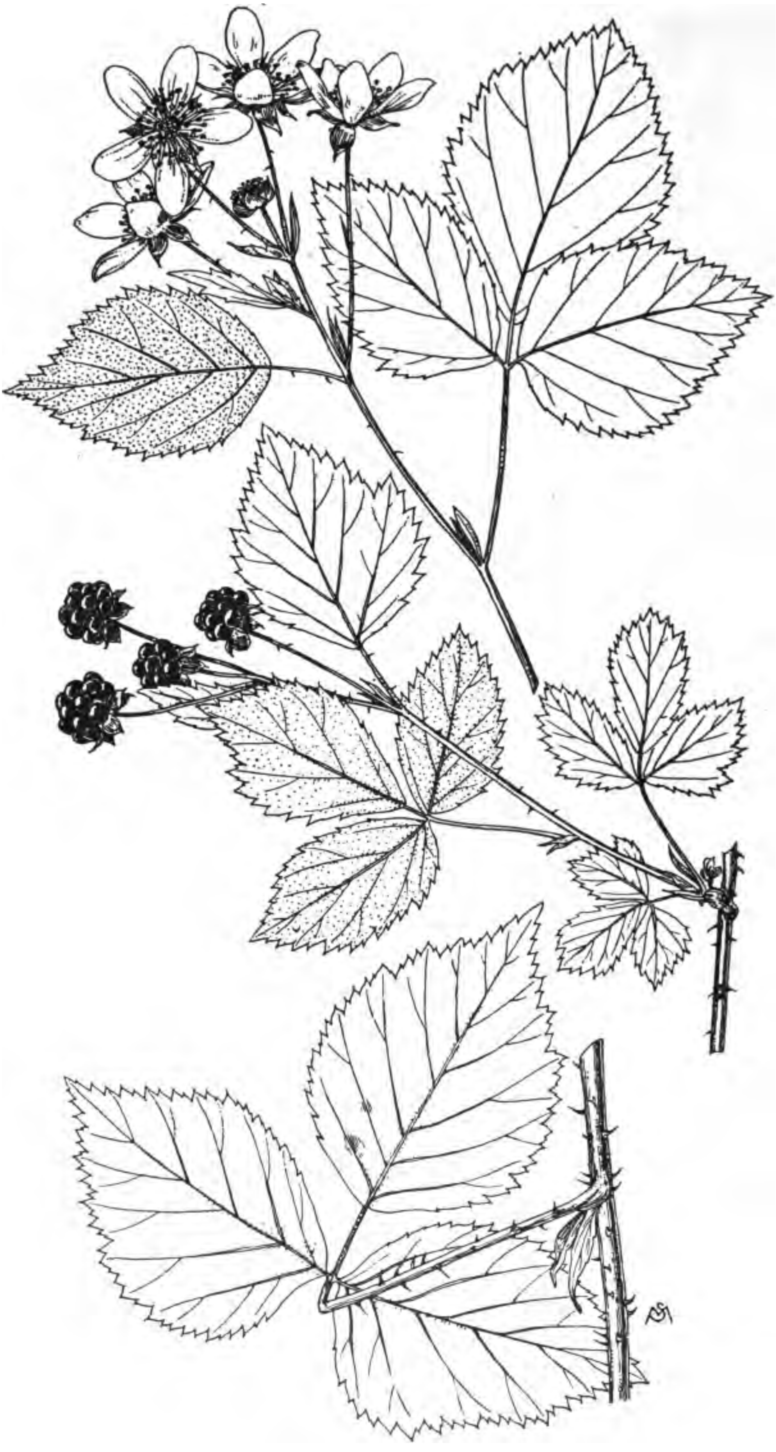


PLATE XXXVI
R. baileyanus X flagellaris
Eight-elevenths natural size.

RUBUS BAILEYANUS X FLAGELLARIS

Rubus invisus (Bailey) Britton, Mem. Torrey Club 4: 115. 1893
Rubus geophilus Blanchard, Rhodora 8: 148. 1906

Stems trailing, 6-12 feet long, glabrous, armed with hooked prickles; cane, leaves and inflorescence glandless; leaves on turions 3-foliolate, of early summer sparsely pubescent beneath, lower leaflets sessile; petiole armed; raceme corymbose, 4-6-flowered; pedicels slightly pubescent, armed with a few scattered prickles; flowers large; fruit globose, black; seeds large.

Resembles *R. baileyanus* in pubescence; resembles *R. flagellaris* in number of prickles on stem and number of flowers in raceme; the shape of leaflets, size of prickles and most other characters are intermediate.

Pollen about 15% imperfect.

Type station: Ithaca, N. Y.

Collected at the following stations: North Hero, Vt.; Burlington, Vt.; Plymouth, Mass.; South Duxbury, Mass.; Rocky Point, R. I.

Following is a list of additional hybrids or suspected hybrids which are found in New England together with a list of the stations where these forms have been collected. Wherever any of these forms have been described as species their binomial is always cited.

Rubus allegheniensis X baileyanus

Stations: Martha's Vineyard, Mass.; Long Island, N. Y.

Rubus allegheniensis X canadensis

Rubus orarius Blanchard, Rhodora 8: 169. 1906

Stations: Stratton, Vt.; Ripton, Vt.

Rubus allegheniensis X frondosus

Stations: Townshend, Vt.; Stratton, Vt.; Walpole, N. H.; Marshall County, Ill.; Indiana (C. C. Deam).

This hybrid is the probable progenitor of the following cultivated varieties: Agawan, Barnard, Erskine Park, Jumbo, Lawton, Snyder, Stone and Wachusett.

Rubus allegheniensis X pergratus

Stations: North Hero, Vt.; West Wardsboro, Vt..

Rubus argutus X canadensis

Rubus amnicola Blanchard, Rhodora 8: 170. 1906

Station: Kennebunk, Me. (type station).

Rubus argutus X enslenii

Rubus ostryifolius Rydberg, Britton Man., 497

Station: Atlantic Highlands, N. J. (type station).

Rubus argutus X hispidus

Station: Hewlett, L. I.

Rubus argutus X setosus

Rubus ascendens Blanchard, Rhodora 9: 9. 1907

Station: Southington, Conn. (type station).

Rubus argutus X vermontanus

Station: Springfield, Mass.

Rubus baileyanus X enslenii

Stations: North Hero, Vt.; Butler's Island, Lake Champlain; Rutland, Vt.; Fair Haven, Vt.; West Wardsboro, Vt.; Walpole, N. H.; Cold River Station, N. H.; Rocky Point, R. I.; South Duxbury, Mass.; Boston, Mass.; Plymouth, Mass.; Rehoboth, Mass.

This hybrid is the probable progenitor of the following cultivated vareties: Bartel, General Grant, Mammoth and Premo.

Rubus baileyanus X canadensis

Rubus multiformis Blanchard, Rhodora 8: 179. 1906 (in part).

Station: Kennebunk, Me.

Rubus baileyanus X hispidus

Stations: West Wardsboro, Vt.; Rocky Point, R. I.; South Duxbury, Mass.; Nantucket Island, Mass. (Bicknell); Woodmere, Long Island, N. Y. (Bicknell); Cypress Hills, Long Island, N. Y.

Rubus baileyanus X setosus

Rubus semisetosus Blanchard, Rhodora 9: 8. 1907

Stations: Plainville, Conn. (type station); Southington, Conn. (Andrews).

Rubus canadensis X elegantulus

Stations: Londonderry, Vt.; Stratton, Vt.

Rubus canadensis X flagellaris

Rubus multiformis Blanchard, Rhodora 8: 179. 1906 (in part)

Station: Kennebunk, Me.

Rubus canadensis X frondosus

Rubus recurvans var. *subrecurvans* Blanchard, Rhodora 8: 152. 1906

Stations: Kennebunkport, Vt. (type station); West Wardsboro, Vt.; Wallingford, Vt.

Rubus canadensis X pergratus

Stations: Burlington, Vt.; Stratton, Vt.; West Wardsboro, Vt.; Londonderry, Vt.; South Londonderry, Vt.; Jamaica, Vt.; Leicester, Vt.; Berkshire, Vt.; Berkshire Center, Vt.; North Windham, Vt.

Rubus canadensis X vermontanus

Stations: Stratton, Vt.; West Wardsboro, Vt.; Ripton, Vt.; Troy, N. H.

Rubus elegantulus X vermontanus

Stations: Stratton, Vt.; West Wardsboro, Vt.; North Windham, Vt.; Stratford, N. H. (Fernald).

Rubus elegantulus X frondosus var. recurvans

Stations: Stratton, Vt.; West Wardsboro, Vt.

Rubus elegantulus X setosus

Rubus groutianus Blanchard, Am. Bot. 10: 108. June, 1906

Stations: West Wardsboro, Vt. (type station); Stratton, Vt.

Rubus enslenii X flagellaris

Station: Nantucket, Mass. (Bicknell).

Rubus enslenii X frondosus

Stations: Nantucket, Mass. (Bicknell); Fairmount, Ind. (C. C. Deam).

The "Illinois" in cultivation is probably to be associated with this hybrid.

Rubus enslenii X hispidus

Station: Nantucket, Mass. (Bicknell).

Rubus enslenii X setosus

Station: Long Island, N. Y.

Rubus flagellaris X frondosus

Rubus plicatifolius Blanchard, Rhodora 8: 149. 1906

Stations: Burlington, Vt.; Middlebury, Vt.; Dummerston, Vt.; Essex, Vt.; Kennebunk, Me.

Rubus flagellaris X hispidus

Stations: Nantucket, Mass.; Long Island, N. Y.

Rubus flagellaris X setosus

Rubus tardatus Blanchard, Rhodora 8: 124. 1906

Station: Kennebunk, Me.

Rubus frondosus X vermontanus

Stations: Manchester, Vt.; Williamsville, Vt.

Rubus hispidus X vermontanus

Rubus cubitans Blanchard, Torreya 6: 148. 1906

Stations: Westminster, Vt. (type station); Stratton, Vt.; West Wardsboro, Vt.

Rubus pergratus X vermontanus

S:ation: Eden, Vt.

Rubus setosus X vermontanus

Rubus vermontanus var. *viridifolius* Blanchard

Stations: Stratton, Vt.; West Wardsboro, Vt.; Townshend, Vt.; Rutland, Vt.; Leicester, Vt.; Banks of Lake Victoria, Ont.

Additional Forms of Doubtful Status

Rubus cuneifolius Pursh, Fl. Am. 347. 1814.
Rubus biformispinus Blanchard, Rhodora 8: 178. 1907.
Rubus rossbergianus Blanchard, Rhodora 9: 7. 1907.
Rubus semierectus Blanchard, Rhodora 8: 156. 1906.
Rubus recurvicaulis Blanchard, Rhodora 8: 153. 1906.

CITATIONS

(1) Britton, N. L. and Brown A. D. Illustrated Flora of the Nort
United States, Canada and the British Possessions. 1913.
(2) Robinson, B. L. and Fernald, M. L. Gray's New Manual of Bo
7th ed. Illustrated. 1911.
(3) Rydberg, P. A. North American Flora. Vol. 22. 1913.
(4) Bailey, L. H. The Standard Cyclopedia of Horticulture. Vol. 5. 1
(5) Sudre, H. Rubi Europae. 1908-1913.
(6) Rogers, M. M. Handbook of British Rubi. 1900.
(7) Lotsy, J. P. Evolution by Means of Hybridization. 1916.
(8) Jeffrey, E. C. Spore Condition in Hybrids and the Mutation Hypot
of DeVries. Bot. Gaz. 58: 322. 1914.
(9) ———— Some Fundamental Morphological Objections to
Mutation Theory of DeVries. Am. Nat. 49: 5. 1915.
(10) ———— Evolution by Hybridization. Memoirs Brooklyn
Garden. 1: 298. 1918.
(11) Bicknell, E. P. Have We Enough New England Blackberries? B
Torrey Club. 37: 393. 1910.
(12) Brainerd, Ezra. The Blackberries of Vermont. Bull. Vt. Bot. C
9: 9. 1914.
(13) Brainerd, Ezra. Blackberries of New England. Rhodora 2: 26. 1
(14) Bailey, L. H. The Evolution of Our Native Fruits. 2nd ed. 368. 1
(15) Card, F. W. Bush-Fruits. Revised ed. 1917.

ity of Vermont and State Agricultural College

mont Agricultural Experiment Station

BURLINGTON, VERMONT

KBERRIES OF NEW ENGLAND---
GENETIC STATUS OF THE PLANTS

By A. K. PEITERSEN

BURLINGTON
FREE PRESS PRINTING COMPANY
1921

THE BOARD OF CONTROL

THE EXECUTIVE COMMITTEE OF THE BOARD OF TRUSTEES
G. W. BAILEY, Burlington.
N. K. CHAFFEE, Rutland.
ROBERT ROBERTS, Burlington.
ELIAS LYMAN, Burlington.
G. M. POWERS, Morrisville.
C. J. WRIGHT, Williston.

THE ADVISORY COUNCIL

HON. ROBERT ROBERTS, Burlington, HON. N. K. CHAFFEE, Rutland,	Representing the University Board of Trustees.
MR. L. K. OSGOOD, Rutland, MR. A. C. WELLS, Bakersfield,	Representing State Grange.
HON. C. W. GATES, Franklin, HON. A. A. DUNKLEE, Vernon,	Representing the Vermont Dairymen's Association.
HON. V. I. SPEAR, Randolph,	Representing the Vermont Sugar Makers' Association.
MRS. G. A DAVIS, Windsor, MRS. J. B. CHASE, Lyndonville,	Representing the Federation of Women's Clubs.
MR. E. B. CORNWALL, Middlebury,	Representing the State Federation of Farm Bureaus.

THE PRESIDENT, DEAN and DIRECTOR, THE DIRECTOR OF THE EXTENSION SERVICE, COMMISSIONER OF EDUCATION and COMMISSIONER OF AGRICULTURE, *Ex-Officio.*

THE OFFICERS OF THE STATION

J. L. HILLS, Sc. D., Director.
C. H. JONES, M. Sc., Chemist.
M. B. CUMMINGS, Ph. D., Horticulturist.
B. F. LUTMAN, Ph. D., Plant Pathologist.
G. P. BURNS, Ph. D., Botanist.
H. B. ELLENBERGER, Ph. D., Animal and Dairy Husbandman.
L. H. FLINT, M. Sc., Assistant Botanist.
E. J. DOLE, A. M., Assistant Botanist.
A. H. GILBERT, M. Sc., Associate Plant Pathologist.
J. A. NEWLANDER, B. S., Associate Dairy Husbandman.
G. F. ANDERSON, Assistant Chemist.
E. W. JENKINS, B. S., Assistant Horticulturist.
ALEXANDER PARKS, Gardener.
WINIFRED B. KENNEDY, Stenographer.
JESSIE L. GUTTERSON, Stenographer.
GUY W. BAILEY, A. B., Treasurer.

☞Copies of the reports and bulletins of the Station are sent free of charge to any address upon application.

☞Address all communications concerning station matters not to individual officers but to the Experiment Station, Burlington, Vt. Address inquiries concerning farm practice to Extension Service, Burlington, Vt.

Director's office, chemical, horticultural and dairy laboratories are in Morrill Hall at the head of Main street; botanical and bacteriological laboratories are at Williams Science Hall, University Place. University farm and buildings are on the Williston road, adjoining the University grounds on the east.

BULLETIN 218: BLACKBERRIES OF NEW ENGLAND—GENETIC STATUS OF THE PLANTS

BY A. K. PEITERSEN*

TABLE OF CONTENTS

I. Scope of the work 5
II. General characters of the Blackberries 6
III. Variations as shown by plants growing wild and those under cultivation 6
IV. Experiments on the influence of External Factors on the development of protodermal outgrowths 7
V. Morphology of protodermal outgrowths 12
VI. Variability and its relation to hybridization 13
VII. Sterility and its relation to interbreeding 13
VIII. Methods used in studying infertility in plants 15
IX. Self-sterility of Rubus as shown by bagging 15
X. Aborted pollen in Rubus 19
XI. Sterility as shown by pollen germination 22
XII. Sterility as shown by hybridization 26
XIII. First generation of artificial hybrids 28
XIV. Segregation in natural hybrids 30
XV. General discussion of the results of the experiment..... 31
XVI. Summary 32

---

*Dr. Ezra Brainerd was associated with Dr. Peitersen during the entire period in which the experimental work reported in this bulletin was under way. His assistance in the field and in the experimental garden was invaluable. His help in naming the individual plants used in the experiments add much to the scientific value of the work.

Dr. Brainerd's knowledge of New England plants gained by years of field study and by extensive experimental work has made him the leading scientific systematic botanist of the genera which he has studied. Hence one can feel certain that the plants used in all the work reported in this bulletin were correctly named.

Dr. Brainerd has been a constant help and inspiration throughout the work and only his modesty keeps us from publishing his name as a joint author.

Bulletin 217 of publications of this Station gave a summary of the work which has been accomplished by the many able workers who have published the results of their labor on the difficult problem of the systematic status of Rubus. These studies followed the ordinary methods of the systematic botanists and led to the most varied conclusions. One does not question the ability of the men who have so faithfully studied this and the other genera of plants, nor does one underrate the value of their work nor the indispensable manuals which they have published, but one does question the "finality of the conclusions" drawn from results obtained by this method. This method necessarily has led to the recognition of so-called "authorities" on the different genera to whom material may be sent for naming. These "authorities" name these plants "by their systematic intuition" gained by long acquaintance with the genus in question. Occasionally there are two authorities in the same field and sometimes they seem to be almost arbitrary in their decisions.

One cannot be surprised that the methods of the systematist has led to confusion in polymorphic genera like Rubus, Cratægus, etc., when one knows that the key published in one of the manuals was made by laying all herbarium material on tables and matching the plants. One would not criticize this method if it is recognized as preliminary work and not taken seriously, but it must be understood that no amount of "systematic intuition" or "prestige as an authority" on Rubus can detect the variations which are due to environment from those which may be of value in a scientific systematic study of the genus. Such preliminary work must be continued, but it is at most only pioneer work and must be subject to revision by the results of carefully conducted experimental work. An herbarium without a botanical garden can add little to our knowledge of the laws of plant development.

The work reported in Bulletin 217 and the present bulletin is an attempt to correlate years of field work with experimental work in garden and greenhouses. Wild plants have been collected, grown under similar conditions, environmental variations evaluated, hereditary factors studied through the segregation of natural hybrids and the production of similar hybrids by artificial crossing, etc. It has been shown that a species which responds to both the recognized systematic and to the genetical criteria for species may arise as the result of hybridization. This shows that hybridization is a potent factor in evolution.

Such experimental work is of the greatest importance and should be used in revising the present manuals. Would that some young man might be induced to undertake such a study of Gratægus!

GEORGE P. BURNS.

SCOPE OF THE WORK

During the summer of 1914 this Station began a series of experiments aiming at the solution of the then perplexing problem of the origin of the many varieties and forms of wild blackberries. At that time it occurred to the writer that data bearing upon this question might have a twofold significance.

First, it might lead to a better and more uniform systematic treatment of the plants in this very polymorphic group. As is stated in Bulletin 217 of this Station, June, 1920, the confused and highly inconsistent treatment accorded this group of plants by the various systematists is in itself excellent evidence of the lack of definite data concerning the origin of many of these doubtful forms. If, therefore, we have succeeded in presenting evidence which will result in a more uniform systematic treatment of the New England wild blackberries, our aim in this respect will have been fully realized.

Second, it was hoped that by an intensive study of the genetic status of the plants in this very variable sub-genus, additional data might be secured which would throw some light upon the evolutionary development of plants in general. It had already been shown experimentally in genera like Viola (Brainerd), and others that natural hybridization occurs frequently. Based only upon systematic differences, Bicknell (2) and others had already named and described a number of wild hybrids of New England blackberries. Part of this work was carried on with the definite aim of either proving or disproving the supposition that blackberries interbreed quite frequently in the wild. It must also be noted in this connection that nearly all of the cultivated varieties of blackberries have quite recently originated from wild forms. Some knowledge of the origin of these forms, therefore, becomes not only important from a purely theoretical point of view but is also fundamental in regard to any future horticultural experimentation aiming at the improvement or production of new varieties.

From extensive field studies it soon became evident that much of the variation in the vegetative characters of these plants was due to external factors. For this reason, the first part of the data presented in the following pages will deal exclusively with such variations. Special attention was also given to the study of sterility occurring within this group, since sterility is unquestionably somewhat correlated with hybridity of origin. The behavior of plants grown from the seed of selfed flowers as well as those grown from the seed of artificially crossed flowers were studied with the expectation that it would throw further light upon the important question of their origin.

GENERAL CHARACTERS OF THE BLACKBERRIES

All New England forms of blackberries have perennial roots and biennial stems; the stems develop the first year and die the second season after flowering and fruiting. The stems range from weak trailers to erect canes from two to three meters high. Their leaves are palmately compound, having as a rule five more or less stalked leaflets, but in some of the dewberry types those of the second year's cane as well as of the first year's cane are trifoliolate or occasionally unifoliolate. Their flowers are born on a more or less contracted cymose-raceme, the terminal flower opening first. The fruit consists of partly cohering drupelets which at maturity break off with the fleshy receptacle. The canes and inflorescence are variously covered with simple hairs, gland-tipped hairs and prickles.

VARIATIONS AS SHOWN BY PLANTS GROWING WILD AND THOSE GROWING UNDER CULTIVATION

The ordinary fluctuating variations, such as the difference in size and shape of leaflets, length of petiole, number of flowers on raceme and differences in other quantitative characters, are familiar to all students of Rubus. There are, however, certain characters which are universally used as a means for distinguishing one species from another which deserves special attention. These are the presence and absence of simple hairs; glandular hairs and prickles; the manner of stem growth, *i. e.*, trailing or erect; the number of leaflets in a leaf; and the tendency of the autumn stems to tip.

Seasonal variations are very pronounced in some species of blackberries. Thus, for example, in most quinquifoliate varieties the early leaves of spring and the late leaves of autumn are nearly always trifoliate or at least show a tendency to develop three leaves instead of five. Similarly in the pubescent species the vernal leaves may be densely pubescent while the leaves of late summer and autumn are sometimes almost glabrous. *R. frondosus* Bigelow is a good illustration of this type of variation.

Some species such as *R. hispidus* L. are noted for their habit of profuse tipping in late autumn. This, however, is a relative character as all blackberries—at least New England species—will tip if grown under favorable conditions for doing so. Even the high-bush blackberry—*R. allegheniensis* Porter—is no exception to this rule.

The manner of stem growth is another character which is greatly emphasized in distinguishing the different species. In order to test the stability of this character, plants of *R. allegheniensis* Porter, *R. setosus* Bigelow, *R. frondosus* Bigelow, and *R. hispidus* L. were grown under three different light conditions, namely, full shade, half shade, and no shade. Full shade was obtained by covering plots with lath nailed on a frame as close together as they would permit when moist; half shade by covering plots with a frame similar to that used for full shade except that every other lath was removed; and no shade by using no covering whatsoever.

Although no definite measurements were made, it was very noticeable that the plants in full shade and half shade grew more erect than the corresponding plants in no shade, the latter showing a very marked tendency to trail. This was especially true in the case of the reclining forms such as *R. frondosus* Bigelow and *R. setosus* Bigelow. Plate I. shows this response to light in the manner of growth in *R. frondosus* Bigelow (plant No. 17-5). The erect cane in the center, which is the old cane, grew in the shade while the trailing stems grew the following year in no shade.

There occur on the blackberries several protodermal or epidermal outgrowths which, according to their various form and size of development, are termed prickles, stalked glands or glandular hairs, gland tipped bristles, and simple hairs (plates II to V, inclusive). The importance assigned to these structures as a means for identification of different species makes a consideration of their development of the utmost importance.

EXPERIMENTS ON THE INFLUENCE OF EXTERNAL FACTORS ON THE DEVELOPMENT OF PROTODERMAL OUTGROWTHS

In the autumn of 1914, suckers from the roots of three plants (No. 7-2, *R. allegheniensis* × *frondosus,* No. 4-1, *R. allegheniensis* Porter and No. 8-2, *R. baileyanus* Britton) were transplanted into large-sized pots containing soil which previously had been made thoroughly uniform by mixing. These were left out of doors until December 1, when they were transferred to four different plots in three different greenhouses. Here they were kept under controlled conditions until April 12, when the experiment was discontinued. All stem growth, therefore, was made during the interval between December 1 and April 12. By the use of three sets of Friez self-recording instruments continuous records were kept of humidity, soil temperature and air temperature during this period for each individual house. Light readings were also taken in the different plots at various intervals of time. Table I gives the average weekly humidity, soil temperature and air temperature of these different plots as well as the total average for the entire period. These weekly averages were computed by using the recorded percentage humidity and degrees temperature at intervals of two hours for the entire week. Of course it must be admitted that averages are often misleading. Since, however, the conditions recorded showed no abrupt variations this method of tabulation was thought sufficiently accurate.

TABLE I. TEMPERATURE, HUMIDITY AND LIGHT CONDITIONS FOR THE DIFFERENT PLOTS

Greenhouse	I			II			III		
	Plot I. Full sunlight			Plot II. Full sunlight			Plot III. and IV. Indirect light		
Week ending	Humidity	Soil temperature	Air temperature	Humidity	Soil temperature	Air temperature	Humidity	Soil temperature	Air temperature
	%	°F	°F	%	°F	°F	%	°F	°F
Dec. 7	67	61	69	59	56	60	68.5	68	68
Dec. 14	56.5	62	70	50.5	56	61	65.5	64	67.5
Dec. 21	56.5	60.5	68	47.5	50	56	57.5	60.5	68
Dec. 28	54	58	65	45	50	56	58	59.5	65
Jan. 4	55	60.5	68	50	51	57	62	63	67
Jan. 11	60	61	68.5	52	53.5	60.5	61.5	66	70.5
Jan. 18	58.5	62	70	47	52.5	60.25	62.5	65	69
Jan. 25	59	60	67	51	51.5	60	63	65	69.5
Feb. 1	57	60	66	50.5	50	57	63.5	62	67
Feb. 8	58.5	60	66.5	50	51.5	61	65	64	70
Feb. 15	57	61	68	52	51.5	59.5	62	65	69.5
Feb. 22	69.5	58	67	55	51.5	60	63	67	73
Mar. 1	77.5	57.5	67	60	51	60.5	68	66.5	71.5
Mar. 8	73	57.5	66	58	50.5	60	66	64	67.5
Mar. 15	80	58	64	59	50	59.5	64	64	68.5
Mar. 22	77.5	59	65	59	50.5	60	70	64	69.5
Mar. 29	77.5	60	64.5	61.5	51	60	69	68	70
Apr. 5	77	58.5	64	60	48	58	71.5	68	71.5
Apr. 12	80	59.5	67	63	52.5	65	69	66	68
Average of the weekly averages	65.84	59.68	66.86	54.21	51.50	59.53	64.71	64.71	68.97

Plants in plots I and II grew in full sunlight under ordinary greenhouse conditions; plants in plot III grew under three layers of cheesecloth, reducing the light value to approximately one-fourth that of plots I and II; while plants in plot IV grew in the same greenhouse as those in plot III but the light value for this plot was approximately three-fifths of that for plots I and II.

At the conclusion of this experiment data were taken on several plants from each of the four plots including the number and development of the glandular hairs and prickles on the stem, petioles and leaflets as well as the leaf area and other characters not tabulated here. Tables II and III (p. 10) give a summary for ten plants grown from the shoots of *R. allegheniensis* × *frondosus* (No. 7-2). This plant was selected because the prickles and glandular hairs as well as the simple hairs are very conspicuous. The plants of *R. allegheniensis* Porter showed similar variations in the number of glandular hairs and prickles. Plate II shows a portion of the stem of a shoot of *R. allegheniensis* × *frondosus* grown in plot III, while plate III shows a corresponding section of a similar plant grown in plot I.

Table II. Number of Protodermal Outgrowths on Plants Grown in the Different Plots

			Glandular hairs			Prickles		
	Length of stem in cm.	No. of leaves on stem	On leaflets	On petioles	On stem	On leaflets	On petioles	On stem
Plot I.								
Plant 1	50	13	1090	988	850	1173	433	165
Plant 2	74	15	1886	1950	2442	1050	407	185
Plot II.								
Plant 1	41	12	2517	3581	1465	1393	603	147
Plant 4	52	13	2007	1755	884	1268	619	130
Plot III.								
Plant 1	118	14	49	24	7	980	305	158
Plant 2	158	18	54	2	0	1386	344	201
Plant 3	145	16	154	36	46	1077	352	190
Plant 4	168	25	192	46	2	1060	385	212
Plot IV.								
Plant 1	43	9	242	83	105	736	254	123
Plant 2	49	14	436	287	124	996	312	146

Since *R. baileyanus* Britton is almost devoid of conspicuous glandular hairs, these plants showed little or no variation in this character, while shoots of this parentage grown in plots I and II showed an increased growth in the number and size of the prickles as compared with those grown in the other plots.

These experiments were repeated during 1915-16, using the same roots but placing them in different plots. Other species, including

R. groutianus Blanchard and *R. frondisentis* Blanchard, were also used. Similar results were obtained for each plot as those of the preceding year.

Hereditary differences were overcome in these experiments by using shoots from the same plant for comparison; and since the soil was uniform for all plots and the water content kept as uniform as possible throughout the growing period, the only principal factors that would vary for the different plots were humidity, temperature and light. Consequently, any variation in the growth of these plants must be in a measure a response on the part of the plant to one or more of these varying factors. By referring to table III a great variation in the number of glandular hairs and prickles will be noted. This variation becomes more apparent if we use for a standard of comparison

$$\frac{\text{total number of glandular hairs}}{\text{total leaf area in sq. cm.}} \text{ and } \frac{\text{total number of prickles}}{\text{total leaf area in sq. cm.}}$$

Table IV gives a summary of these values and the varying factors for each plot. A study of this table will show that temperature is not to any material extent a determining factor in the formation of glandular hairs and prickles. Plants grown in plots I and III with a comparatively small difference in temperature show a large differ-

TABLE III. SUMMARY OF THE TOTAL NUMBER OF GLANDULAR HAIRS AND PRICKLES AND TOTAL LEAF AREA FOR PLANTS IN THE DIFFERENT PLOTS

	Glandular hairs	Prickles	Leaf area in sq. cm.
Plot I.			
Plant 1	2928	2143	2156.47
Plant 2	6278	1642	2717.40
Plot II.			
Plant 1	7563	2143	2156.47
Plant 4	4646	2017	2108.81
Plot III.			
Plant 1	80	1443	2997.12
Plant 2	56	1931	4261.58
Plant 3	236	1619	3863.41
Plant 4	240	1657	2572.65
Plot IV.			
Plant 1	430	1113	1500.63
Plant 2	847	1450	2784.02

ence in the development of glandular hairs and prickles (plates II and III). Humidity, which has been considered a very important factor in the formation of spines and spinescent emergencies, does not seem to affect their development as greatly as might be expected. In plots where the average humidity was about the same, the plants showed a wide variation in the production of glandular hairs and prickles; and in like manner for plots III and IV. The only remaining variable, namely, light, must, therefore, be the main determining factor. And it will be noted that the number of these outgrowths on the different plants for each plot is almost in direct proportion to the intensity of the light. This is partly in agreement with the work of Lothelier and others (3, 4, 5). A corresponding variation in the abundance of simple hairs also occurred but is not tabulated here.

It was thought that irritation, such as a plant growing in a windy

TABLE IV. A COMPARISON OF THE NUMBER OF PROTODERMAL OUTGROWTHS AND THE CONDITIONS UNDER WHICH THE PLANT WAS GROWN

	Average humidity	Average soil temperature	Average air temperature	Comparative light values	Total number of prickles / Total leaf area sq. cm.	Total number of glandular hairs / Total leaf area sq. cm.
Plot I.	%	°F	°F			
Plant 1					92	153
Plant 2					60	231
Average	65.84	59.68	66.86	1	76	192
Plot II.						
Plant 1					99	350
Plant 4					95	220
Average	54.21	51.50	59.53	1	97	285
Plot III.						
Plant 1					48	2
Plant 2					45	1
Plant 3					41	6
Plant 4					64	9
Average	64.71	64.71	68.97	.25	49.5	4.5
Plot IV.						
Plant 1					74	28
Plant 2					52	30
Average	64.71	64.71	68.97	.6	63	29

station would be subjected to, might be a factor in the production of protodermal outgrowths. To test this supposition, shoots were tied to a lever which was attached to a water-motor in such a manner as to give the plant a swaying motion, imitating the motion of a shoot blown to and fro in the wind. This treatment, however, had no apparent effect upon the development of hairs or prickles.

The taxonomic value of simple hairs, glandular hairs and prickles in this genus is not questioned; yet it is evident from the preceding data that only by comparative study of plants grown under essentially similar conditions can these structures furnish a reliable criterion for classification.

MORPHOLOGY OF THE PROTODERMAL OUTGROWTHS

The prickle, glandular hair, and simple hair are all protodermal or epidermal outgrowths, and the primordia of all three structures are present in all New England species of blackberries. The glandular hairs and prickles are especially conspicuous in all seedlings (plate IV, fig. 7). They may remain rudimentary as is the case of the glandular hairs on the same species (plate IV, fig. 4) and thus their presence may not be noted in the mature plants.

The simple hairs are unicellular structures (plate IV, fig. 2). These develop from certain cells from the outer layer of the protoderm which at first become conspicuous by the enlargement of their nuclei (plate IV, fig. 1) and, later, by a tangential elongation.

The glandular hairs, as well as the prickles, have a similar origin. The cell primordia of these structures, however, do not show an enlargement of their nuclei, but at an early stage undergo a tangential division (plate IV, fig. 3). These cells may then divide both periclinally and anticlinally (plate IV, fig. 6) resulting in the formation of a glandular hair or prickle. In some instances, two or more protodermal cells may enter into the formation of these structures (plate IV, fig. 5), but this does not in any way alter their development. There is no morphological difference between the glandular hair and the prickle except that in the former the terminal cells change into large, secretive organs. The prickle is often, though not always, a development from the glandular hair (plate V, fig. 1), so that every glandular hair is a potential prickle.

VARIABILITY AND ITS RELATION TO HYBRIDIZATION

Unusual variability in plants and animals is generally regarded by students of genetics as almost conclusive evidence of hybridity of origin. The practical breeder has long recognized this fact. The main purpose of artificial hybridization is to "break up the continuity of the germ plasm" (6), thus bringing about greater plasticity in the individual plants or animals of the resulting progeny.

If plasticity in the individual is a mark of hybridity of origin, the variations which occur in the growth of the blackberries as shown in the preceding data is a striking evidence of the hybrid origin of the blackberries.

STERILITY AND ITS RELATION TO INTERBREEDING

Absolute or partial sterility has long been recognized as a mark of hybridity of origin. Gärtner (7), as early as 1849, pointed out this peculiarity in hybrids. It is so common a character among plants of hybrid origin and it is so universally recognized as the result of interbreeding that little need be said concerning this phenomenon at this point. One need but refer to the various articles dealing with the productivity of our common cultivated fruits, which are largely of hybrid origin, to find convincing data in support of this general assertion (8, 9). There are, to be sure, apparent isolated instances of perfectly fertile hybrids, as shown by Rosen (10) and others. An interesting example of this occurred in our cultures. In 1914, No. 12-3, *R. vermontanus* Blanchard was crossed with No. 14-5, *R. jacens* Blanchard. Both parent plants produced pollen which was only about 15 percent morphologically perfect (plate VIII, fig. 1 and plate XI, fig. 1). The resulting plants from this cross, however, produced about 90 percent morphologically perfect grains (plate XI, fig. 2). The percentage of fertile ovules was also very much greater in the offspring than in either of the parent plants. Such cases, however, are but exceptions and not the rule and it may possibly be shown later, when our conception of hybrids becomes more definite, that even these may not be exceptions.

Some of our prominent students of genetics contend that absolute fertility in the offspring is a convincing proof that the parents are specifically alike. Bateson (11), as expressed in his very able work, believes that "complete fertility of the results of interbreeding is and must be regarded as inconsistent with actual specific difference." This, however, must not be interpreted to mean that sterility in a certain plant, no matter what may have been its cause, is an absolute proof of its hybridity.

Jeffrey (12, 13, 6, 14), and his students (15, 16), in several quite recently published articles on plant morphology as bearing on evolution, hold the view that a certain type of sterility, *i. e.*, aborted pollen, in a certain species is in itself sufficient proof of its hybridity. His conclusions are, however, based upon quite crude though extensive investigations of this phenomenon and may thus be subjected to serious criticism.

In view of this attributed correlation between hybridity of origin and sterility, the following studies were undertaken with the expectation that they might throw some light on the important subject of interbreeding as it occurs in this group and that they might also furnish some data in regard to the origin of some of the many doubtful species of Rubus. All the material used for this work was obtained either from carefully labeled plants growing in the wild which, afterwards, were transplanted to the Vermont Station gardens, or from plants similarly obtained which had been transferred to the gardens during the preceding year. This procedure would seem to eliminate, so far as was humanly possible, any error in naming the plants, since they were verified not only as they grew in the wild, but also as they grew under cultivation where they could be studied during the entire season. It may be argued that by transplanting the plants and placing them under cultivated conditions the spore formation powers of these plants might be materially affected. This, however, we have not found to be the case.

It must be remembered that sterility may result from various causes. It may be due to purely external factors, such as injury to the pistils or stamens by frosts, insects, etc. (17). It may result from a lack of proper pollination, that is to say, pollination may take place too late, too early, or not at all. Such types of infertility, however, have very little significance as evolutionary factors although they may be vitally important to the practical horticulturist. On the other hand, infertility may be due to defects in the formation of the microspore or megaspore and their resulting gametophytes, or it may be due to the lack of functional power in the male or female elements. These last mentioned types of infertility are fundamental variations in respect to the perpetuation of any particular species. They are, therefore, important in a consideration of this group.

METHODS USED IN STUDYING INFERTILITY IN PLANTS

Infertility, especially among cultivated plants, has been quite extensively investigated. Probably the oldest method (18) and one that is in common use at the present time, is that of bagging the flowers. A bag of paper or other material is placed over the unopened flower and permitted to remain until the fruit has "set." By this method quite reliable data can be obtained in regard to self-fertility, although if relied upon exclusively it may be subject to serious criticism, as will be shown later.

Since cytological technique has come into common usage several workers, especially Dorsey (19) and Lutz (20), have used this method in studying sterility and by its use valuable data concerning this phenomenon have been obtained. It has been shown by this method that sterility among flowering plants in the majority of cases is due to the degeneracy of the microspores. Degeneracy in the pistil is quite rare. This has led to a careful study of the formation and development of the microspore. In some instances the percentage of aborted pollen has been used as an index of sterility (15, 6) while in others the capability of microspore germination in some artificial media has been likewise used (17, 22, 23).

Aside from these methods, a comparative study of the results of cross- and close-pollination has added greatly to our knowledge of sterility in plants.

SELF-STERILITY OF RUBUS AS SHOWN BY BAGGING

For this work only plants growing in the gardens were used. In this way it would seem that more accurate data concerning the comparative infertility of the different so-called species could be obtained than if the same work had been done in the field where the plants inevitably would be growing under quite different conditions. Parchment bags were used. These were placed over the flowers one or two days before the flowers opened and left until the fruit had "set." Only fully developed seeds were counted.

It has been noted among other groups of the flowering plants that fertilization occurs more readily when the pollen from the flower on a different part of the same plant is used for pollination than if the pollen from the same flower is used. In the clovers Westgate (24) finds this difference to be very great. This does not seem to be the case in the Rubus studied. Quite extensive comparisons in this respect were made with a number of plants including the following species: *R. allegheniensis* Porter, *R. frondosus* Bigelow, *R. canadensis* L. and *R. setosus* Bigelow. Little or no difference in the number of seeds formed per flower were noted. For the sake of uniformity, however, only four or five flowers were enclosed in each bag.

Table V gives a detailed list of the plants used in this work together with the number of flowers bagged and those not bagged on each plant and table VI summarizes the data.

TABLE V. SHOWING RESULTS OF CLOSE AND INSECT POLLINATION

No.	Plant name	Bagged		Not bagged	
		Number of flowers	Number of seed formed	Number of flowers	Number of seed formed
4-1	R. *allegheniensis* Porter	48	0	36	1260
202-1	R. *allegheniensis* Porter	23	0	45	1832
125-1	R. *allegheniensis* Porter	141	0	84	2940
212-1	R. *allegheniensis* Porter	7	0	203	5175
120-1	R. *allegheniensis* × *argutus* (andrewsianus Blanchard)	8	15	16	192
120-3	R. *allegheniensis* × *argutus* (andrewsianus Blanchard)	14	26	8	95
13-4	R. *allegheniensis* × *canadensis*	7	16	32	835
310-1	R. *allegheniensis* × *canadensis*	8	16	30	793
13-1	R. *allegheniensis* × *canadensis*	16	20	122	310
13-3	R. *allegheniensis* × *canadensis*	126	182	4	28
13-4	R. *allegheniensis* × *canadensis*	136	109	1	9
13-6	R. *allegheniensis* × *canadensis*	330	340	8	43
46-1	R. *allegheniensis* × *elegantulus* (R. flavinanus Blanchard)	48	93	41	615
46-2	R. *allegheniensis* × *elegantulus* (R. flavinanus Blanchard)	15	36	63	1003
7-2	R. *allegheniensis* × *frondosus*	149	6	506	3669
204-1	R. *allegheniensis* × *hispidus* (R. permixtus Blanchard)	13	0	17	183
205-1	R. *allegheniensis* × *hispidus* (R. permixtus Blanchard)	13	14	82	8341
213-1	R. *baileyanus* Britton	28	6	47	612
8-1	R. *baileyanus* Britton	5	1	11	163
216-1	R. *baileyanus* Britton	16	19	28	291
13-2	R. *canadensis* L.	80	80	68	1714
13-5	R. *canadensis* L.	42	37	14	368
133-1	R. *canadensis* × *setosus* (R. junceus Blanchard)	16	21	14	11
105-1	R. *elegantulus* × *setosus* (R. groutianus Blanchard)	12	0	15	129
105-2	R. *elegantulus* × *setosus* (R. groutianus Blanchard)	12	2	31	235
105-3	R. *elegantulus* × *setosus* (R. groutianus Blanchard)	14	2	7	27
105-8	R. *elegantulus* × *setosus* (R. groutianus Blanchard)	9	0	33	429
31-1	R. *elegantulus* × *setosus* (R. groutianus Blanchard)	6	1	7	28

111-1	*R. flagellaris* × *setosus* (R. tardatus Blanchard)	16	17	23	59
7-3	*R. frondosus* Bigelow	62	211	25	513
17-1	*R. frondosus* Bigelow	11	31	62	591
17-2	*R. frondosus* Bigelow	7	24	11	96
17-3	*R. frondosus* Bigelow	10	17	26	248
17-4	*R. frondosus* Bigelow	14	60	24	254
17-5	*R. frondosus* Bigelow	12	21	114	657
121-3	*R. frondosus* Bigelow (R. brainerdi Rydb.)	10	12	15	129
137-1	*R. frondosus* × *setosus* (R. abbrevians Blanchard)	18	42	6	138
137-3	*R. frondosus* × *setosus* (R. abbrevians Blanchard)	62	155	18	396
38-1	*R. hispidus* L.	9	0	12	1
203-1	*R. hispidus* L.	9	0	44	457
209-1	*R. hispidus* L.	14	34	106	1021
14-1	*R. hispidus* × *setosus* (R. jacens Blanchard)	23	0	400	96
14-2	*R. hispidus* × *setosus* (R. jacens Blanchard)	4	1	260	16
14-3	*R. hispidus* × *setosus* (R. jacens Blanchard)	31	1	12	2
14-4	*R. hispidus* × *setosus* (R. jacens Blanchard)	8	0	234	14
14-5	*R. hispidus* × *setosus* (R. jacens Blanchard)	16	1	781	29
14-6	*R. hispidus* × *setosus* (R. jacens Blanchard)	130	8	594	77
101-3	*R. hispidus* × *setosus* (R. jacens Blanchard)	10	1	18	132
1-1	*R. hispidus* × *setosus* (R. trifrons Blanchard)	24	2	417	1547
117-1	*R. hispidus* × *setosus* (R. trifrons Blanchard)	120	7	262	833
117-2	*R. hispidus* × *setosus* (R. trifrons Blanchard)	40	3	42	304
32-1	*R. hispidus* × *setosus* (R. trifrons Blanchard)	7	0	3	33
48-2	*R. pergratus* Blanchard	48	13	44	794
48-3	*R. pergratus* Blanchard	112	34	36	643
119-6	*R. setosus* Bigelow	42	116	20	64
119-2	*R. setosus* Bigelow	26	83	85	578
12-1	*R. vermontanus* Blanchard	82	52	1056	6135
12-2	*R. vermontanus* Blanchard	51	2	419	568

One must not rely too much upon the data set forth in these tables. Any attempt to correlate these figures with the amount of sterility in a given species would be highly unscientific. It is obvious that when the flowers are bagged fertilization must take place under very much more unfavorable conditions than under normal conditions. Not only are the temperature, humidity and light factors greatly changed, and it has been shown by Sandsten (17) that these affect the development of the microspore materially, but it might also be argued that the chances for proper pollination were greatly reduced by enclosing the flowers in bags. It was shown, however, that the shaking of the bags by the wind effectively pollinated the flower. And since

TABLE VI. SUMMARY OF DATA GIVEN IN TABLE V.

Name	Average number of seed formed per flower when bagged	Average number of seed formed per flower when not bagged
R. allegheniensis Porter	0.00	30.45
R. andrewsianus Blanchard	1.86	11.95
R. orarius Blanchard	1.09	10.24
R. flavinanus Blanchard	2.04	15.55
R. allegheniensis × *frondosus*	.04	7.25
R. permixtus Blanchard	.53	86.10
R. baileyanus Britton	.53	12.39
R. canadensis L.	.95	25.39
R. junceus Blanchard	1.31	.78
R. groutianus Blanchard	.09	9.11
R. tardatus Blanchard	1.06	2.56
R. frondosus Bigelow	3.13	9.00
R. brainerdi Rydb.	1.20	8.60
R. abbrevians Blanchard	2.46	22.25
R. hispidus L.	1.06	9.12
R. jacens Blanchard	.05	.15
R. trifrons Blanchard	.06	3.75
R. pergratus Blanchard	.29	17.96
R. setosus Bigelow	2.92	6.11
R. vermontanus Blanchard	.40	4.54

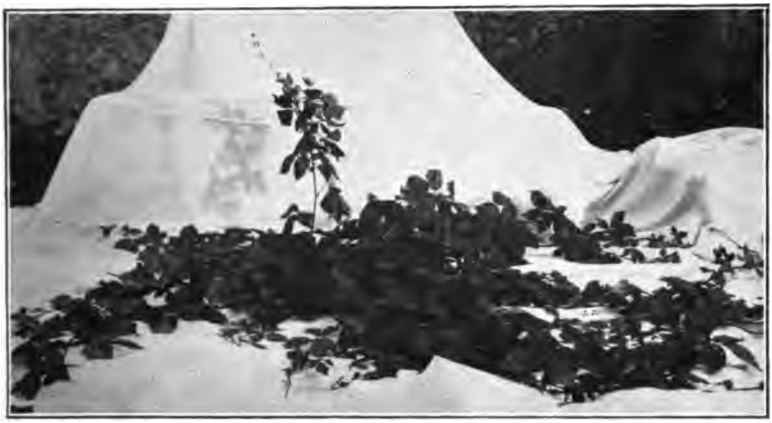
only the comparative sterility of the different species was sought, these and other factors would not materially affect the value of the data.

Another factor which would make the data obtained by this method valueless is the quite uncommon phenomenon of apogamy. This, however, does not occur in the Rubus studied or it would have become apparent both in the latter cytological studies as well as in the checks used in connection with the cross-pollination work (table XII, p. 27).

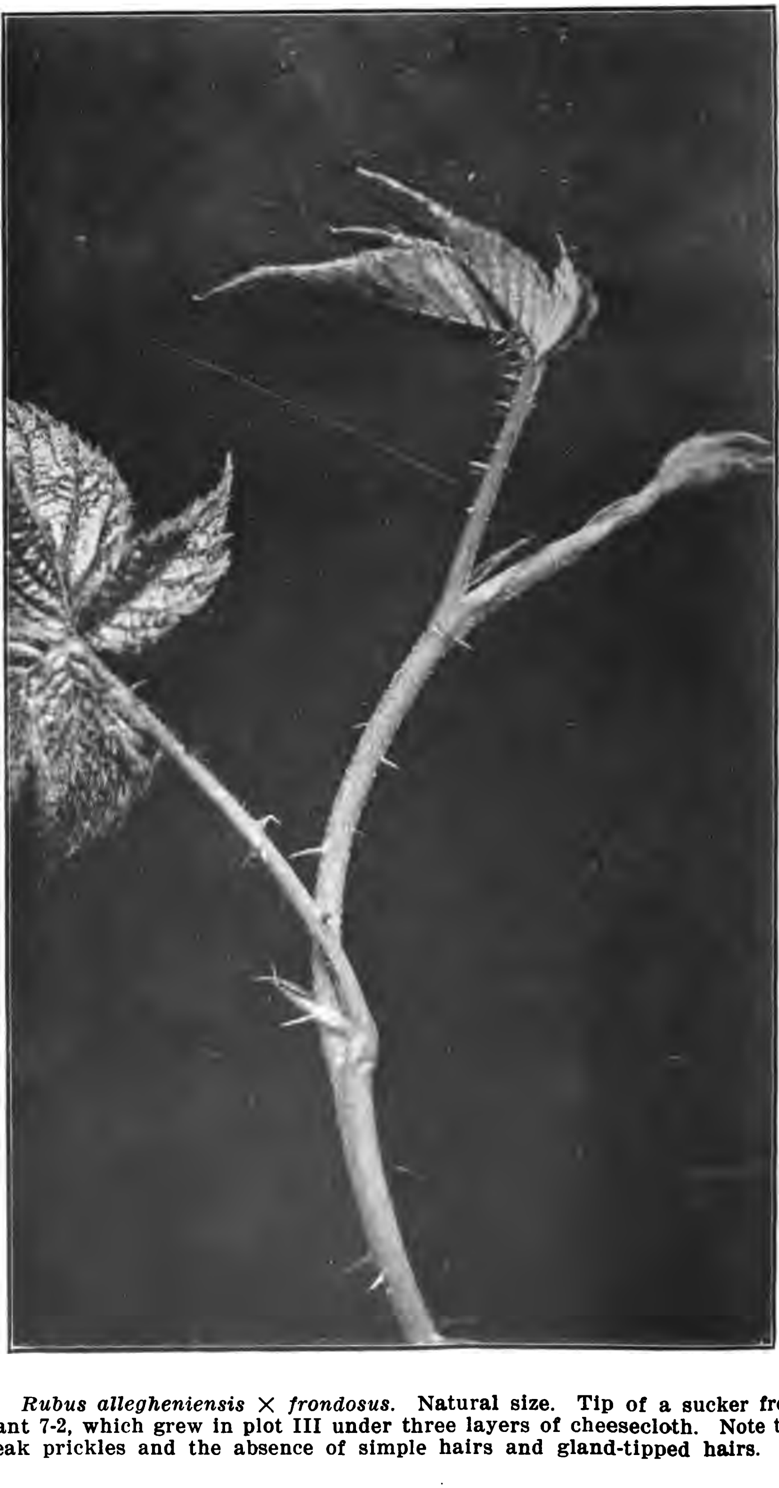
From a study of tables V and VI three facts become very apparent. These are also corroborated by the results obtained by other methods which will be referred to later.

1. A large percentage of infertility occurs in most of the blackberries. The amount of infertility, as shown in table VI in the case of the flowers not bagged, ranges from an average of only 86.10 fertile ovules per flower in *R. permixtus* Blanchard to almost complete sterility in the case of *R. jacens* Blanchard. It will also be noted that in general the greatest percentage of sterility is found among well-recognized hybrids as *R. allegheniensis* × *frondosus, R. junceus* Blanchard, *R. trifrons* Blanchard and *R. jacens* Blanchard. Those showing least infertility are the distinct and universally recognized species, like *R. alleghenienses* Porter, *R. canadensis* L., and *R. baileyanus* Britton.

PLATE I.

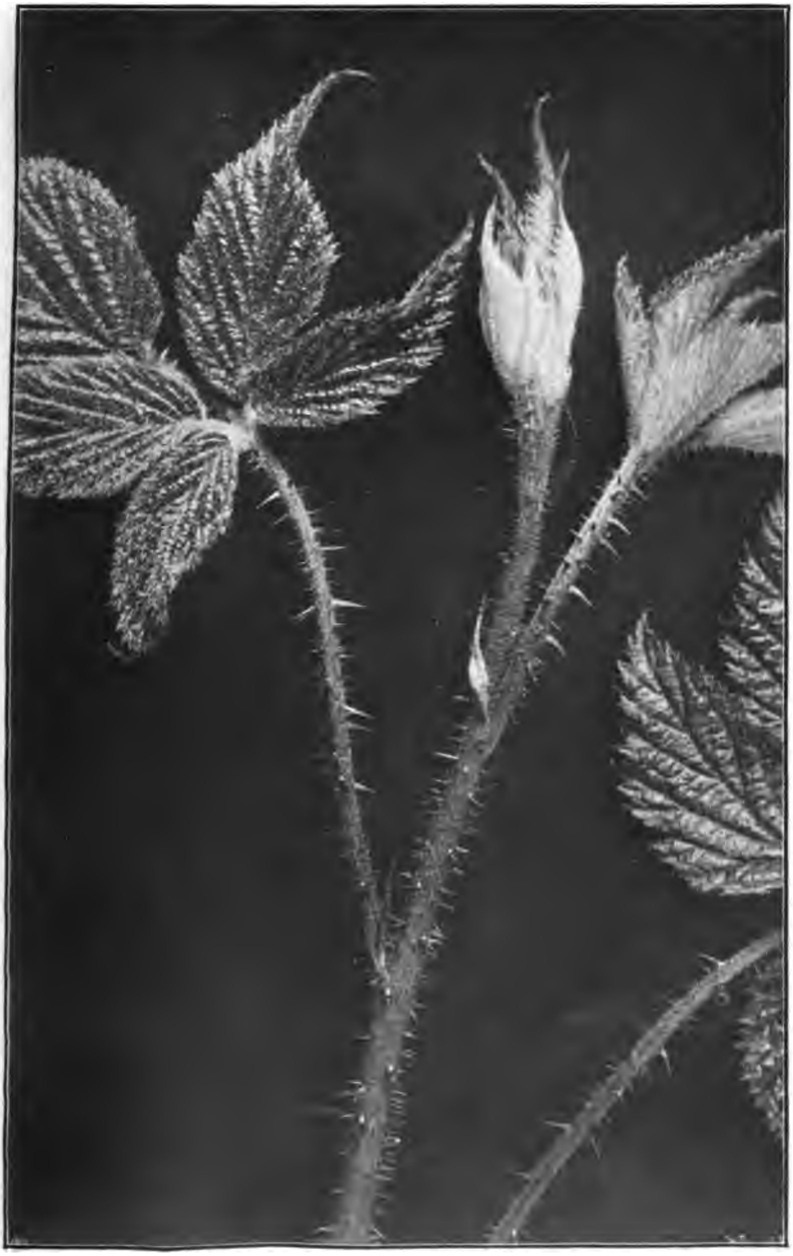


Rubus frondosus Bigelow, 17-5, showing response to light. The erect cane at the center (which is the old cane) grew in the shade, while the trailing stems grew the following season in no shade.



Rubus allegheniensis × *frondosus.* Natural size. Tip of a sucker from plant 7-2, which grew in plot III under three layers of cheesecloth. Note the weak prickles and the absence of simple hairs and gland-tipped hairs.

PLATE III.



Rubus allegheniensis × *frondosus*. Natural size. Tip of a sucker from plant 7-2, which grew in plot II in full sunlight. Note the abundance of simple hairs, gland-tipped hairs and prickles.

PLATE IV.

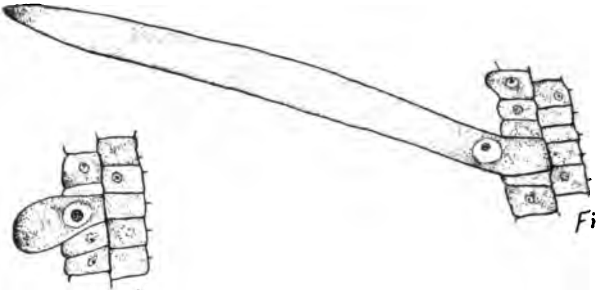


Fig. 2

Fig. 1

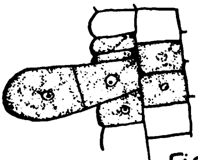


Fig. 3

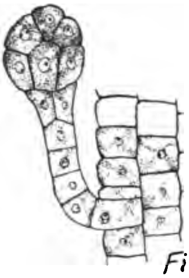


Fig. 4

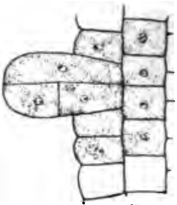


Fig. 5

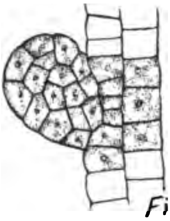


Fig. 6

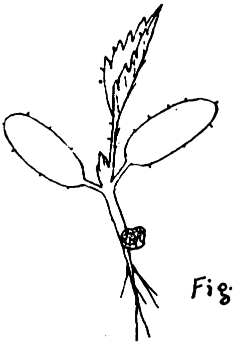


Fig. 7

Figure 1. *Rubus allegheniensis* Porter. A section through the outer portion of growing tip showing the enlarged protodermal cell, which may later develop into a simple hair as shown in figure 2. X 665.

Figure 2. *Rubus allegheniensis* Porter. Showing the enlarged cell of the protoderm developed into a simple hair. X 665.

Figure 3. *Rubus allegheniensis* Porter. Showing a tangential division of a protodermal cell which may later develop into either a prickle or a glandular hair. X 665.

Figure 4. *Rubus canadensis* L. Showing an aborted glandular hair. These are present on all blackberries. X 665.

Figure 5. *Rubus allegheniensis* X *frondosus*. Showing two protodermal cells entering into the formation of a glandular hair or prickle, one having already divided while the other has not. X 665.

Figure 6. *Rubus allegheniensis* Porter. Showing the result of the rapid periclinal and anticlinal divisions of the protodermal cell which will later develop into a conspicuous glandular hair or prickle as shown in plate V, fig. 1. X 665.

Figure 7. *Rubus canadensis* L. Showing glandular hairs and prickles on seedling. X 2.

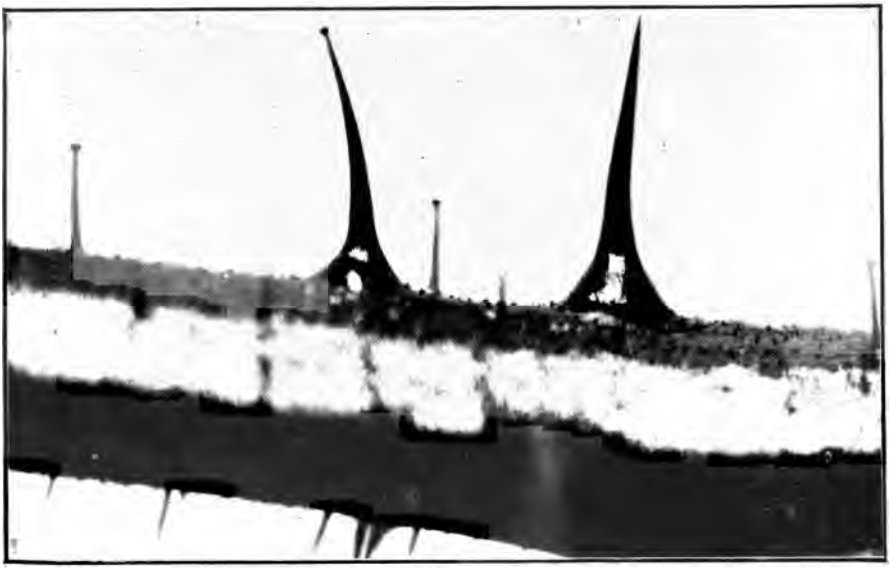


Figure 1. *Rubus allegheniensis* Porter showing the numerous aborted gland-tipped hairs, the normally developed gland-tipped hairs, the gland-tipped hair developed into a prickle with the gland still remaining at the tip (at center) and a normally developed prickle. Photographed and enlarged six diameters.

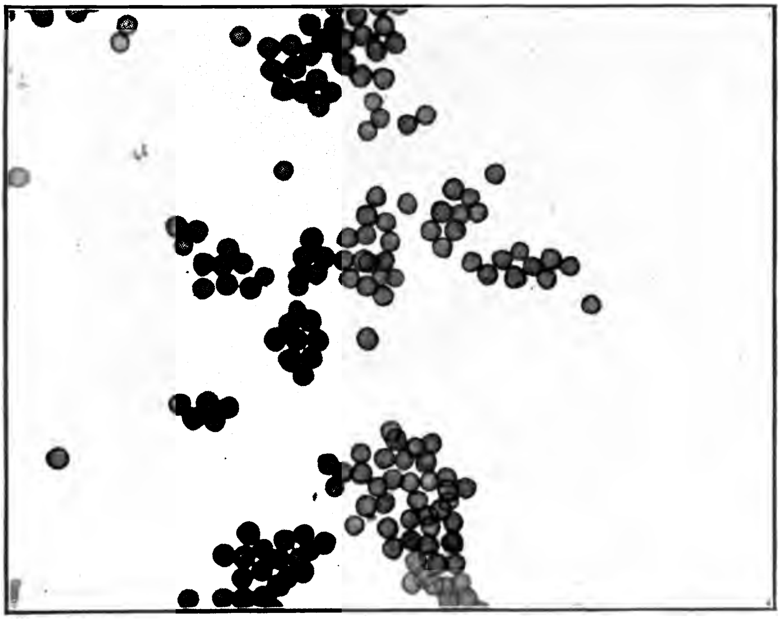


Figure 2. Micro-photograph of pollen grains of *Rubus allegheniensis* Porter, 125-1, a pubescent form. X 85.

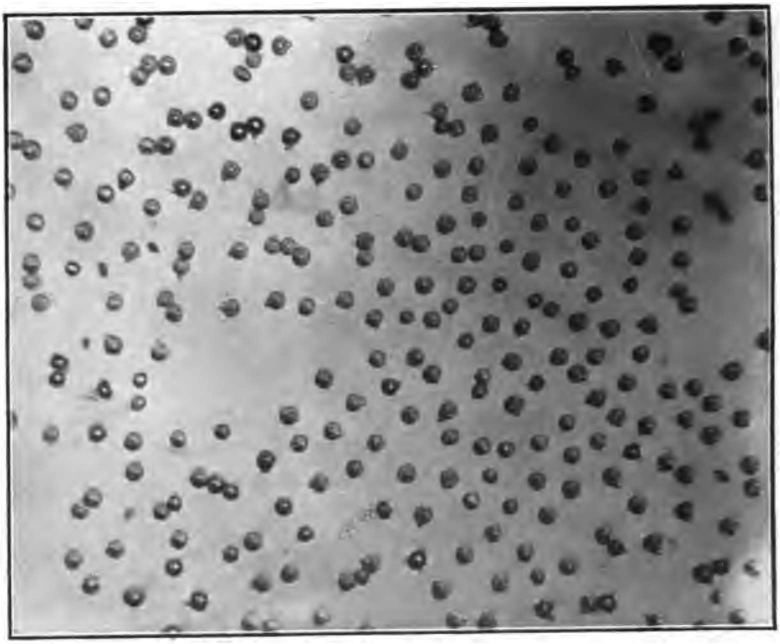


Figure 1. Micro-photograph of pollen grains of *Rubus allegheniensis* Porter, 4-1. X 85.

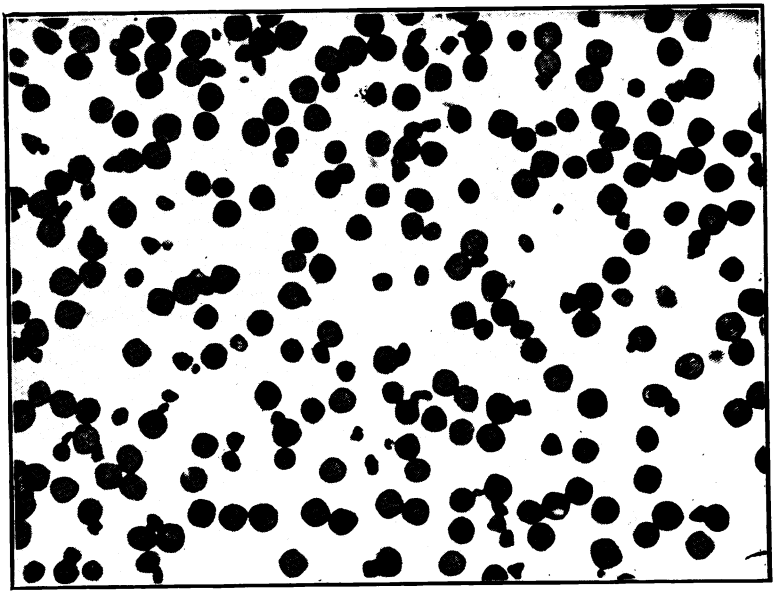


Figure 2. Micro-photograph of pollen grains of *Rubus pergratus* Blanchard, 48-3. X 85.

PLATE VII.

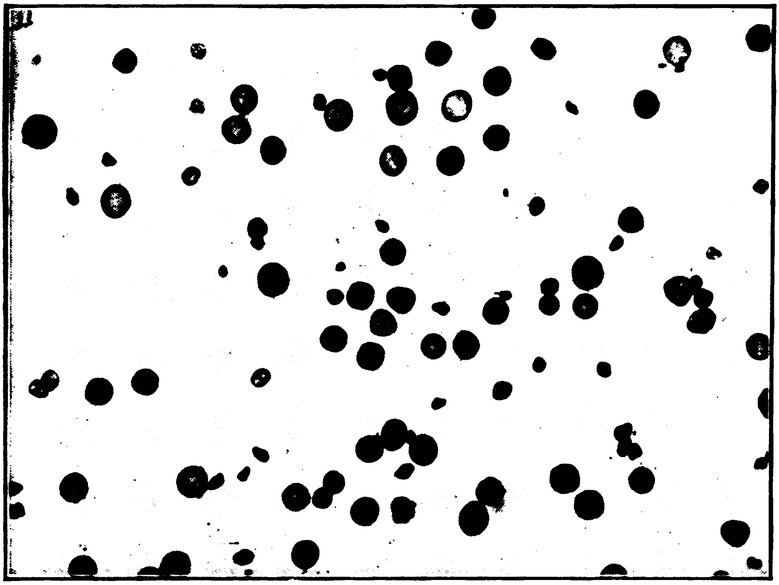


Figure 1. Micro-photograph of pollen grains of *Rubus frondosus* Bigelow, 17-4. X 85.

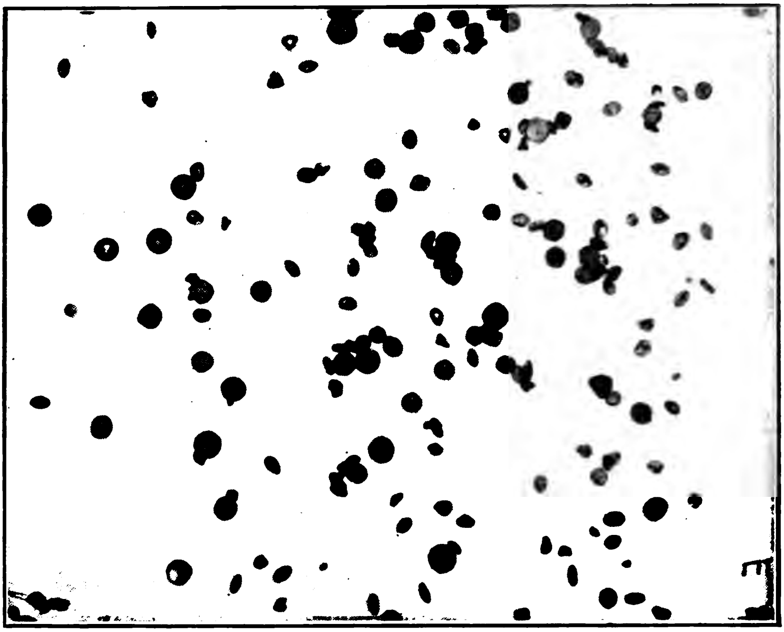


Figure 2. Micro-photograph of pollen grains of *Rubus canadensis* L., 13-5. X 85.

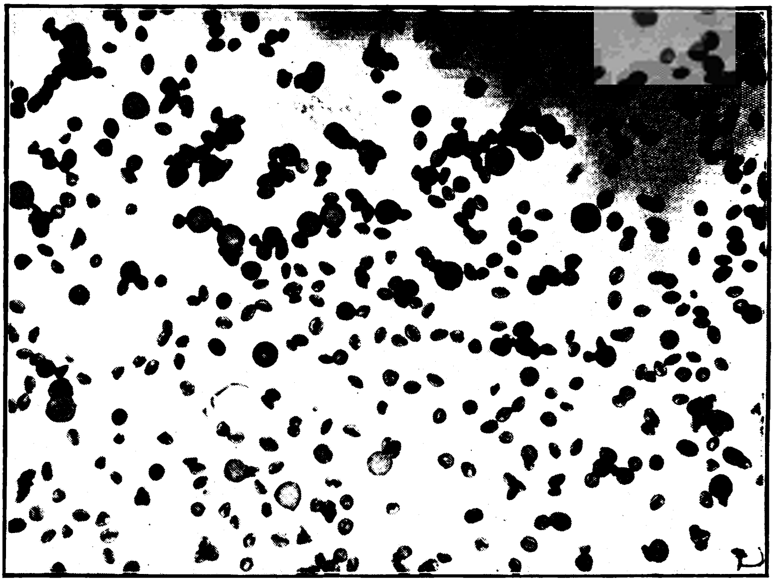


Figure 1. Micro-photograph of pollen grains of *Rubus vermontanus* Blanchard, 12-3. X 85.

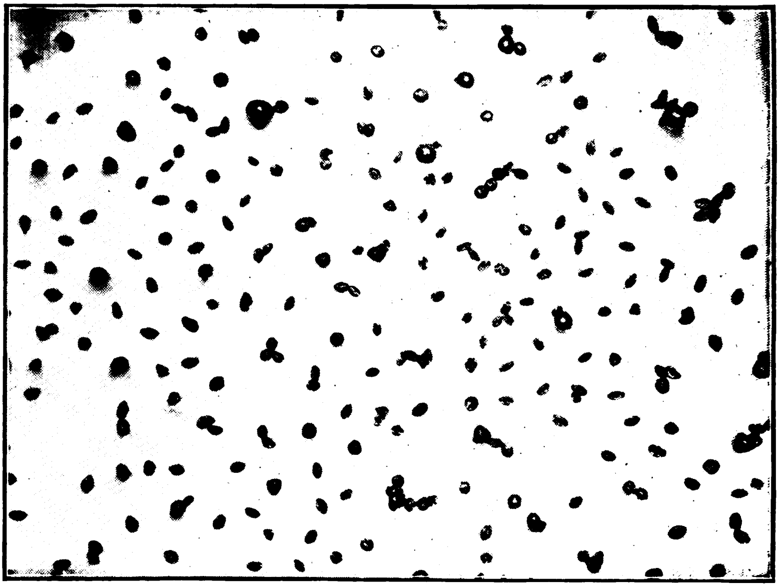


Figure 2. Micro-photograph of pollen grains of *Rubus hispidus* L., 203-1. X 85.

PLATE IX.

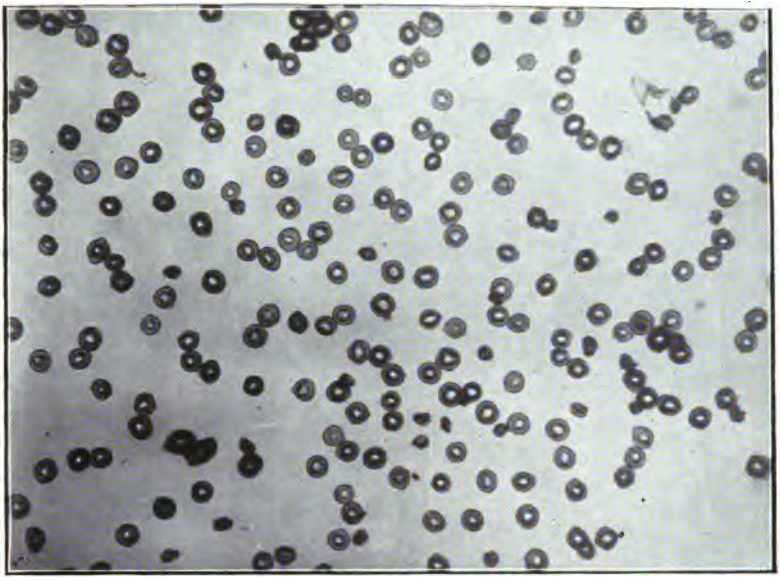


Figure 1. Micro-photograph of pollen grains of *Rubus baileyanus* Britton, 216-1. X 85.

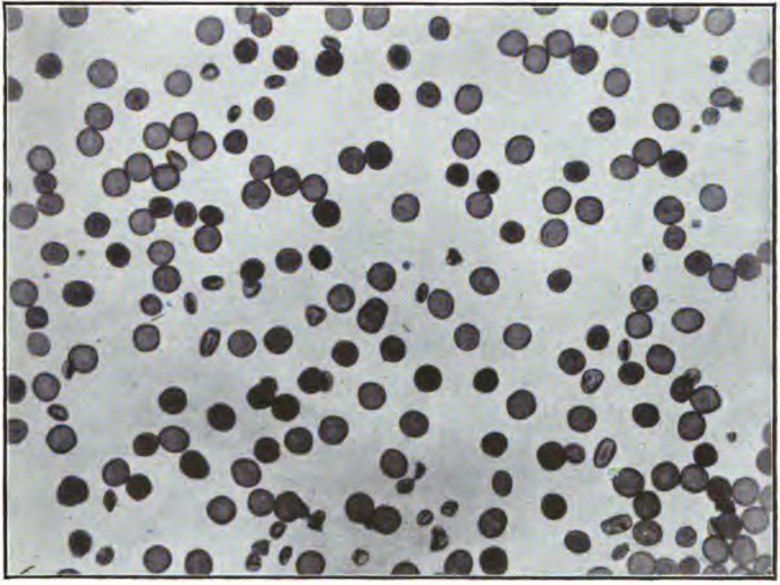


Figure 2. Micro-photograph of pollen grains of *Rubus flagellaris* Willd., 252-2. X 85.

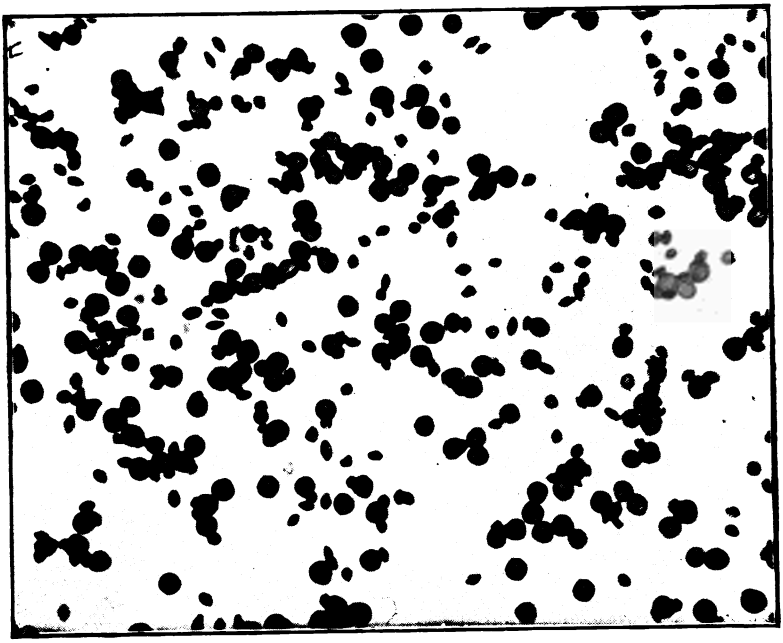


Figure 1. Micro-photograph of pollen grains of *Rubus allegheniensis* × *canadensis*, 13-1 (*Rubus orarius* Blanchard). X 85.

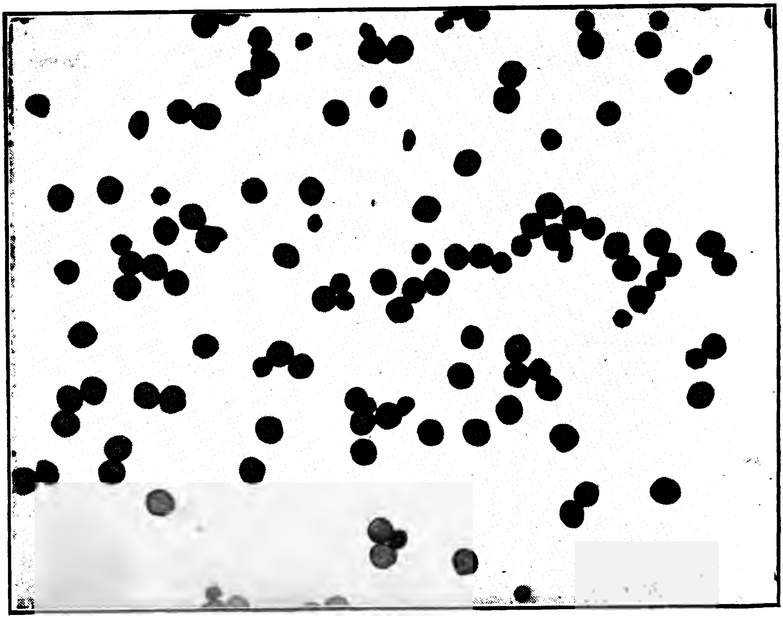


Figure 2. Micro-photograph of pollen grains of *Rubus baileyanus* × *flagellaris*, 252-4 (*Rubus invisus* [Bailey] Britton). X 85.

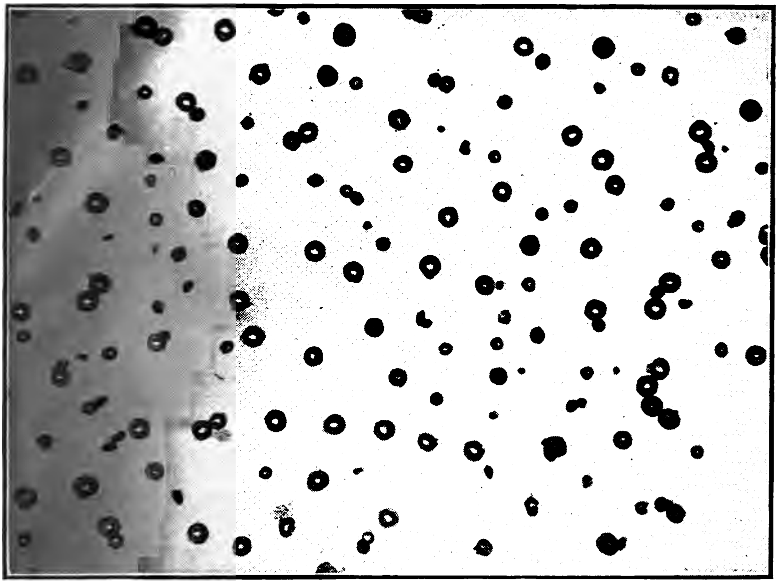


Figure 1. Micro-photograph of pollen grains of *Rubus hispidus* × *setosus*, 14-5 (*Rubus jacens* Blanchard). X 85.

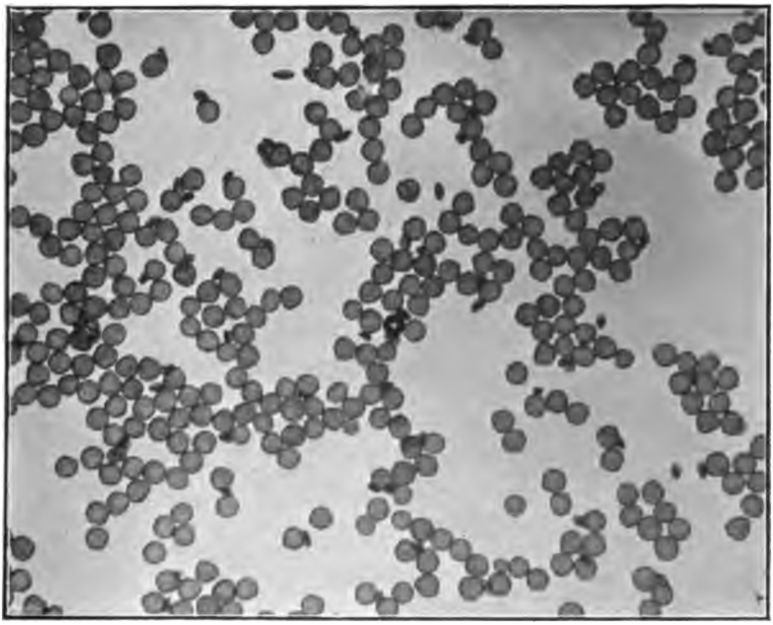


Figure 2. Micro-photograph of pollen grains of plant number 1005-4, which is a seedling whose maternal parent is *Rubus vermontanus* Blanchard, 12-3, and whose paternal parent is *Rubus jacens* Blanchard, 14-5. X. 85. Note the large percentage of morphologically perfect pollen. Compare with plate VIII, fig. 1, and plate XI, fig. 1, which shows the pollen of its two parents.

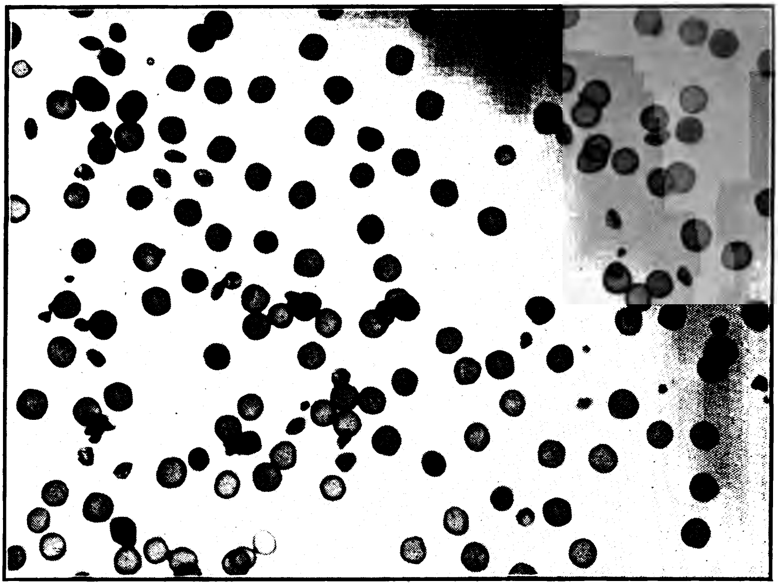


Figure 1. Micro-photograph of pollen grains of *Rubus pergratus* × *setosus*, 136-2 (*Rubus frondisentis* Blanchard). X 85.

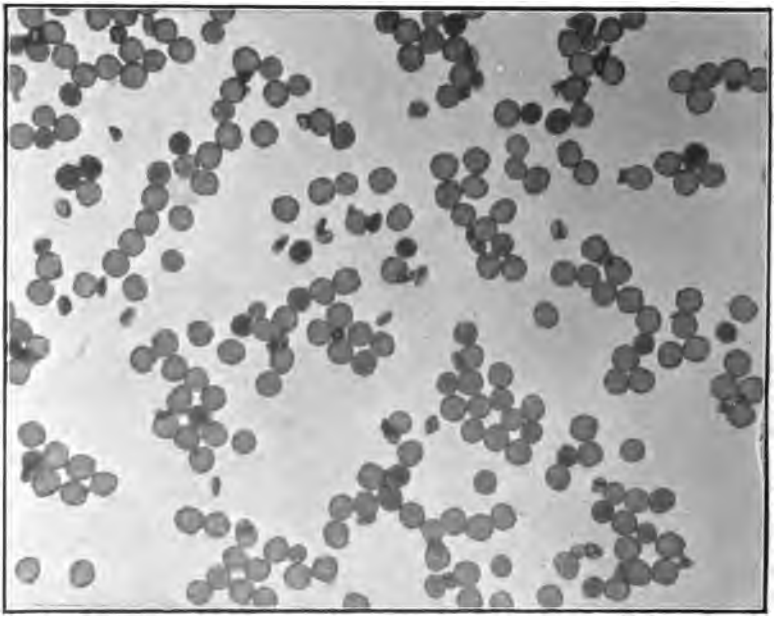


Figure 2. Micro-photograph of pollen grains of *Rubus frondosus setosus*, 137-1 (*Rubus abbrevians* Blanchard). X 85.

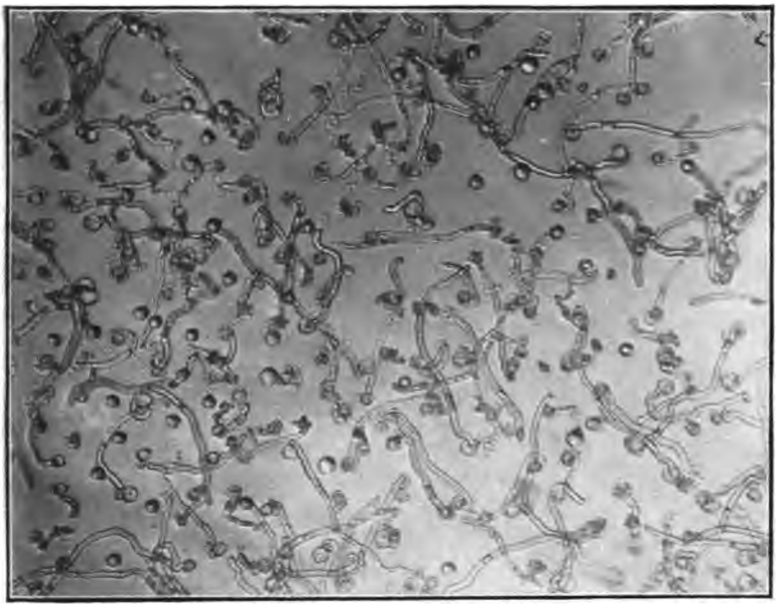


Figure 1. Micro-photograph of pollen grains of *Rubus allegheniensis* Porter, 4-1. Germinated in a hanging drop culture of 12 percent cane sugar solution for three hours. X 85.

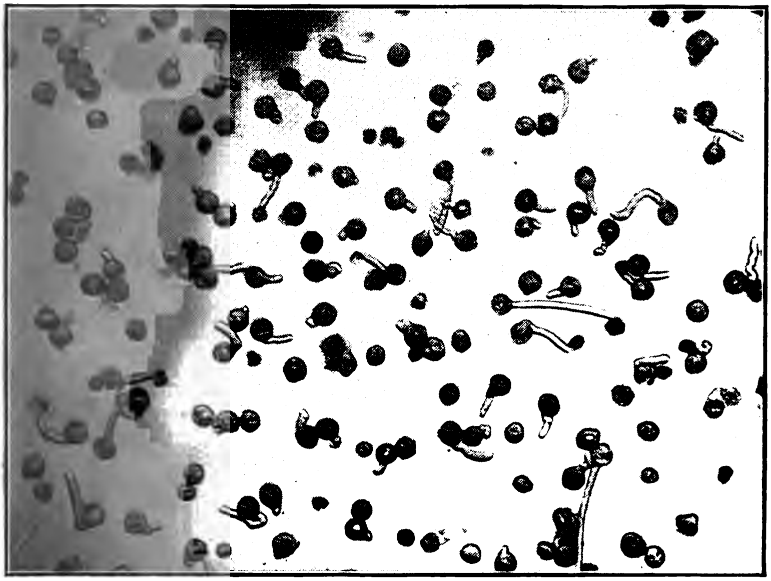


Figure 2. Micro-photograph of pollen grains of *Rubus baileyanus* Britton, 216-1. Germinated in a hanging drop culture of 12 percent cane sugar solution for one hour. X 85.

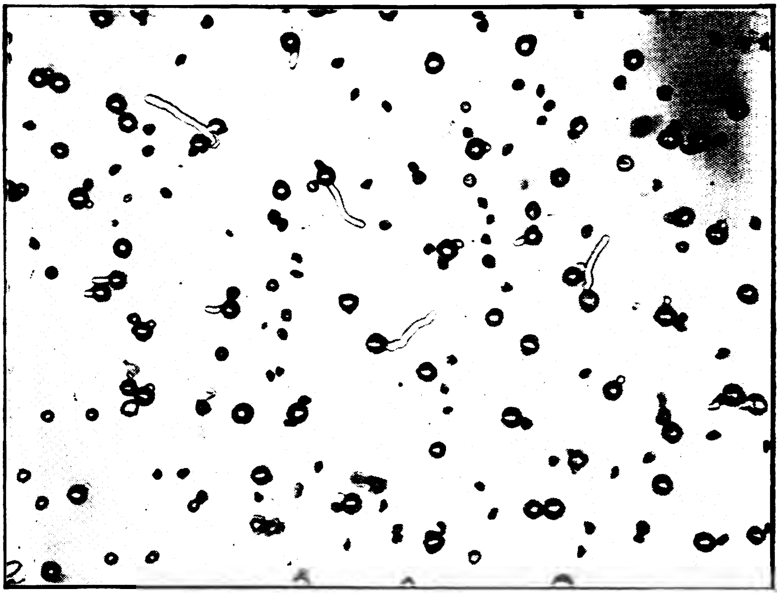


Figure 1. Micro-photograph of pollen grains of *Rubus frondosus* Bigelow, 17-4. Germinated in a hanging drop culture of 12 percent cane sugar solution for four hours. X 85.

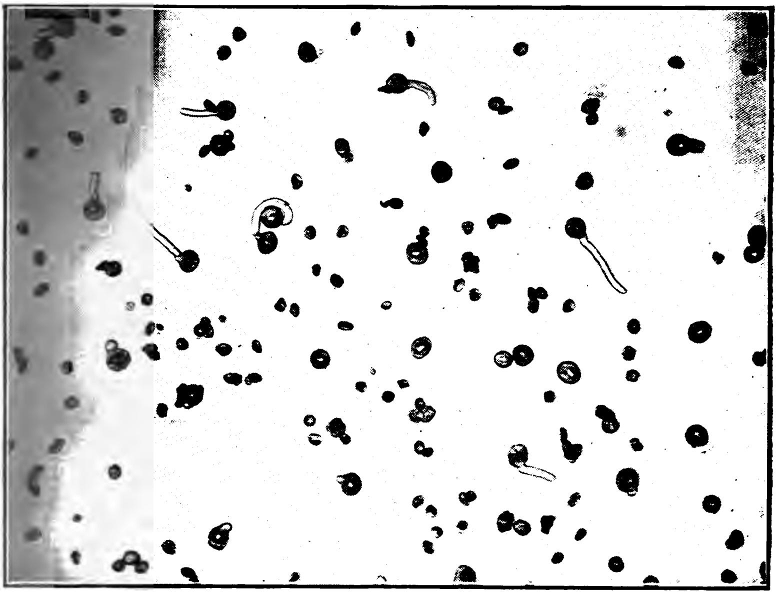


Figure 2. Micro-photograph of *Rubus brainerdi* Rydb., 121-1. Germinated in a hanging drop culture of 12 percent cane sugar solution for one hour. X 85.

PLATE XV.

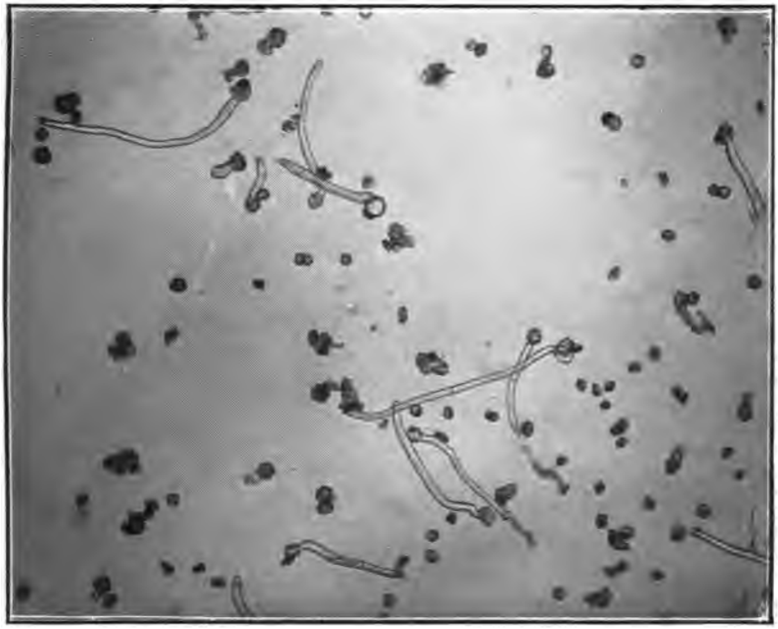


Figure 1. Micro-photograph of pollen grains of *Rubus setosus* Bigelow, 119-2. Germinated in a hanging drop culture of 12 percent cane sugar solution for 12 hours. X 85.

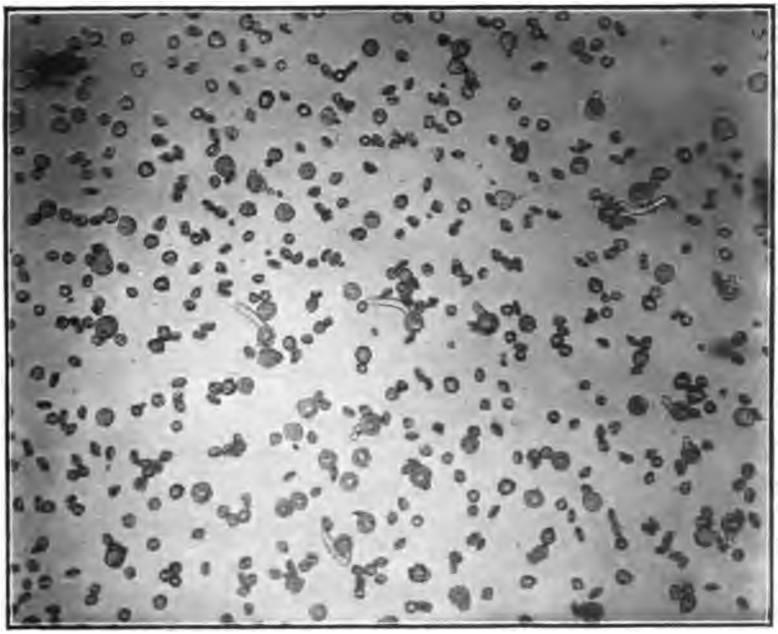


Figure 2. Micro-photograph of pollen grains of *Rubus vermontanus* Blanchard, 12-3. Germinated in a hanging drop culture of 12 percent cane sugar solution for three and one-half hours. X 85.

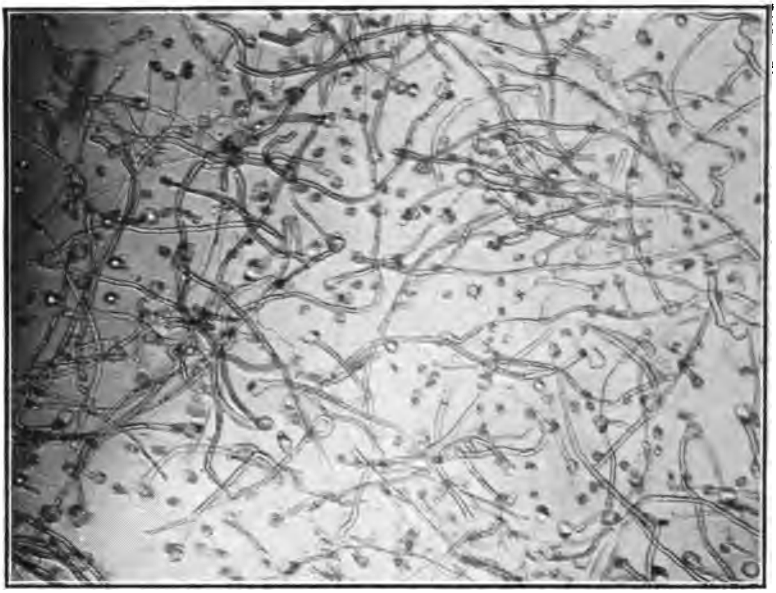


Figure 1. Micro-photograph of pollen grains of *Rubus allegheniensis* × *hispidus*, 205-1 (*Rubus permixtus* Blanchard). Germinated in a hanging drop culture of 12 percent cane sugar solution for 24 hours. X 85.

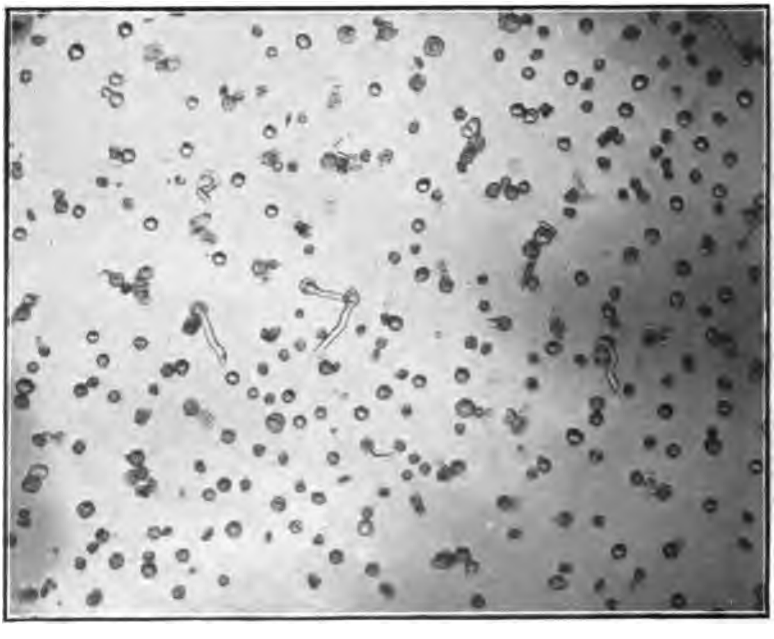
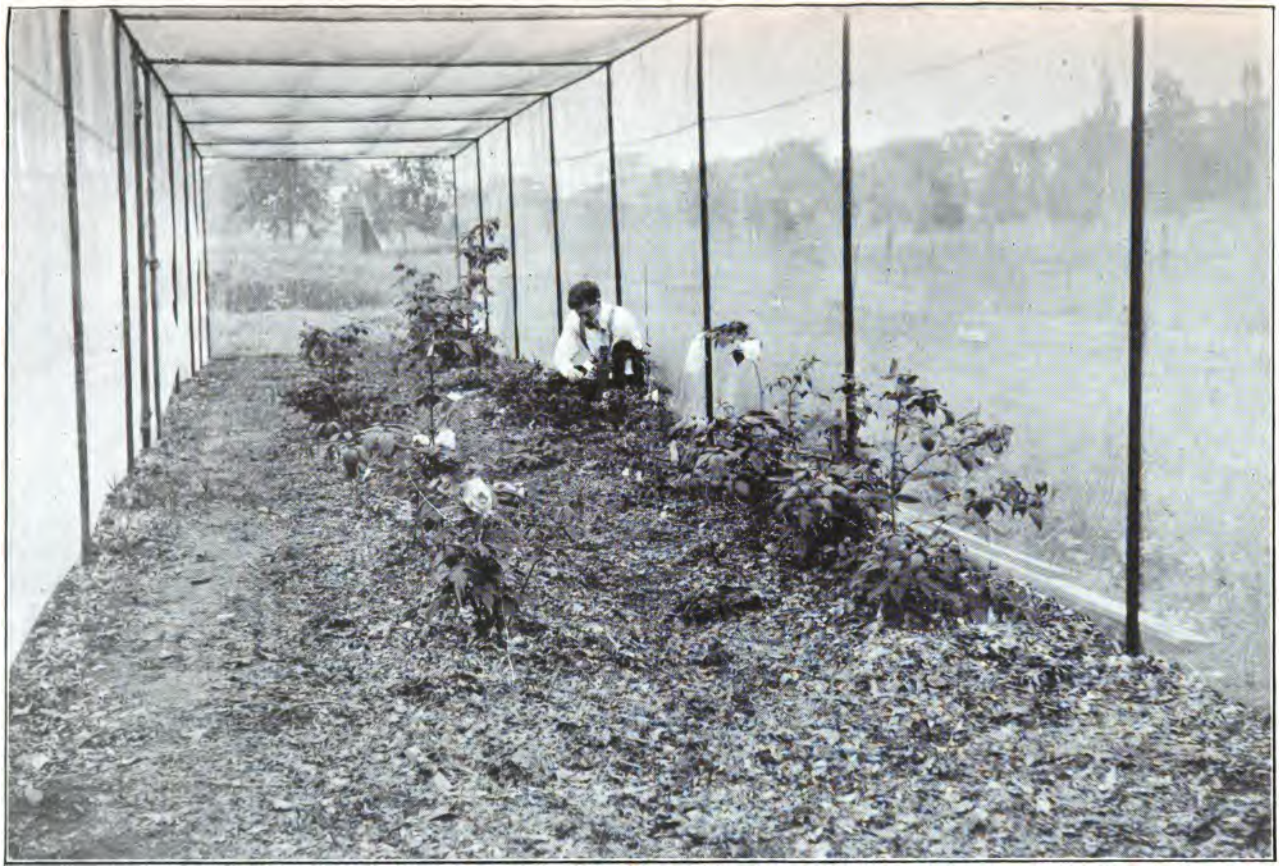
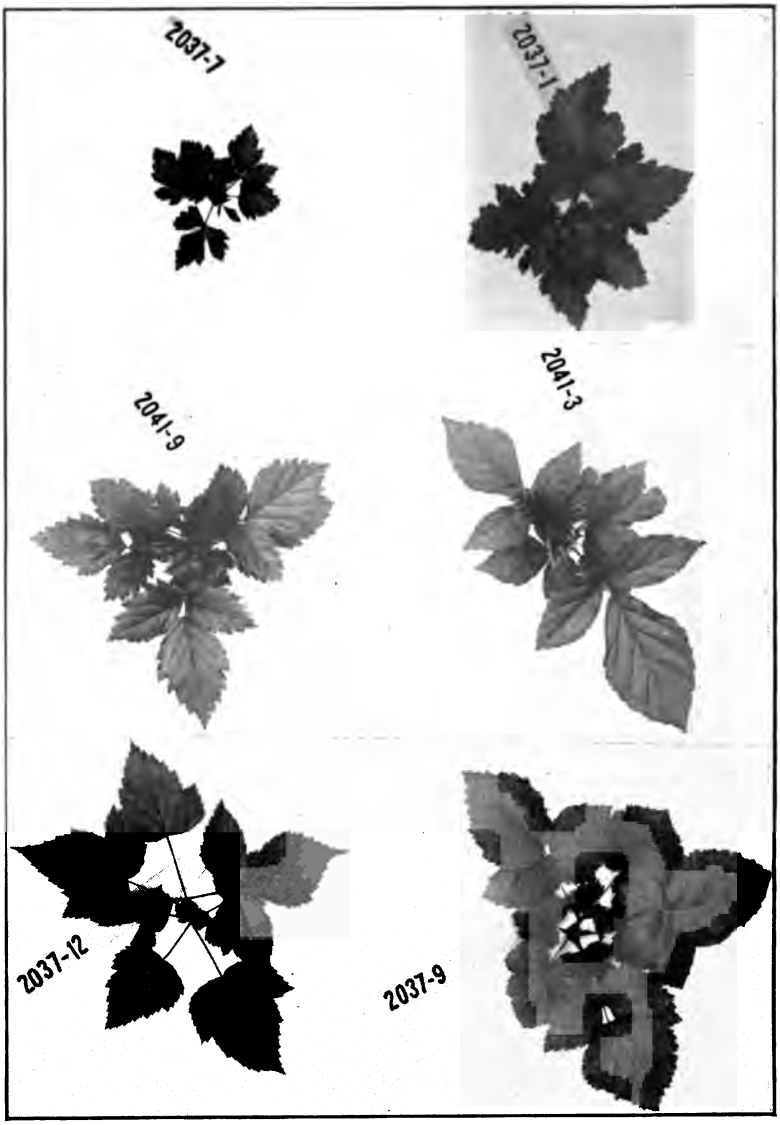


Figure 2. Micro-photograph of pollen grains of *Rubus allegheniensis* × *frondosus*, 7-2. Germinated in a hanging drop culture of 12 percent cane sugar solution for one hour. X 85.



Inside view of cage at Vermont Experiment Station in which the hybridization work was done.

PLATE XVIII.

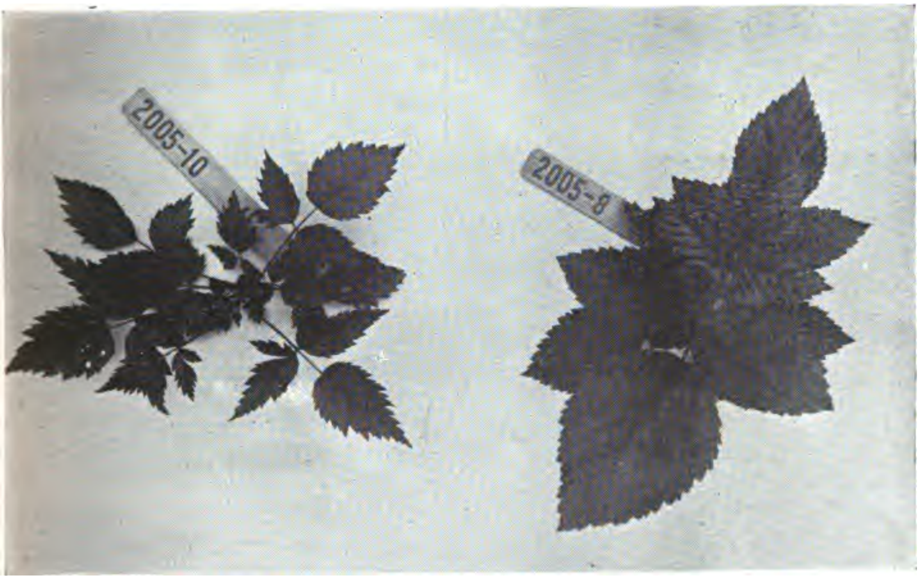


Seedlings from selfed flowers of natural hybrids showing segregation.

Plants Nos. 2041-9 and 2041-3 were grown from seed of selfed flowers of No. 14-2 *Rubus jacens* Blanchard. Plant No. 2041-9 is an almost perfect reversion to *Rubus setosus* Bigelow, while plant No. 2041-3 is a reversion to *Rubus hispidus* L.

Plants Nos. 2037-1, 2037-7, 2037-9 and 2037-12 were grown from seeds of selfed flowers of No. 7-1, *R. allegheniensis* × *frondosus*. Showing some of the different variations in the shape of the leaves.

PLATE XIX.



Rubus allegheniensis × *frondosus*

Two seedlings from selfed flowers of plant No. 122-1, which is a suspected natural hybrid showing reversions to the parent types. Plant No. 2005-8 shows a reversion towards *Rubus frondosus* Bigelow in the orbicular shape of its terminal leaflet. Plant No. 2005-10 shows a reversion towards *Rubus allegheniensis* Porter in having a narrow, ovate terminal leaflet. These are the two extreme variants.

2. The percentage of infertility in any given species or distinct form is quite constant. In some instances this may seem quite contradictory to the data given. As for example, in *R. trifrons* Blanchard, five plants show a very high percentage of infertility, while five others are comparatively quite fertile. In this case we have two distinct forms of *R. trifrons* Blanchard. One form—*R. jacens* Blanchard in part—has a very shiny leaf and in other characters resembles somewhat the dewberry type, while the other form has more of the character of *R. setosus* Bigelow. These two distinct forms of *R. trifrons* Blanchard were noted and labeled as such long before these experiments were begun. This, however, only emphasizes the fact that the percentage of infertility in a given plant is a very important taxonomic character.

3. All species of Rubus studied are either completely self-sterile or nearly so, as shown by the results obtained by bagging the flowers. There may be some chance of error in these figures, as has already been pointed out, although other studies with the same plants bear out the accuracy of these tabulated results.

A very interesting fact in reference to *R. allegheniensis* Porter is here shown. These plants which represent the most monotypic species in the whole blackberry group and whose pollen is morphologically more perfect than any of the others (table VIII, p. 21) were completely self-sterile. Numerous other attempts were made to close fertilize these plants but all failed. An explanation of the cause of self-sterility found in some monotypic forms of plants has been attempted by various workers, but all that may be concluded from the data here presented is that most blackberries are more or less completely self-sterile.

ABORTED POLLEN IN RUBUS

It has been found that sterility among the plants studied is largely due to the degeneration of the microspores after the second division of the spore-mother cell has been completed. This degeneration of the microspore after its initial formation by the homotypic division of the spore-mother cell results in the development of aborted or sterile pollen grains. These aborted grains are present to a more or less extent in all blackberries (plates V to XII, inclusive) and may be readily seen by the aid of a low power microscope if the mature pollen is mounted in water or a sugar solution.

This type of sterility is common among other groups of flowering plants according to different investigators (20, 13, 15). It is a common phenomenon among hybrid or cryptohybrid forms. According to Bateson (11) it is an indication of the hybrid origin of the particular plant in which it is found.

The pollen from available forms of blackberries growing in the Vermont Station gardens was examined and the percentages of aborted pollen grains were computed. This was done by mounting the pollen from the anthers of newly unfolded flowers in a 12 percent solution of cane sugar. The eye-piece of the microscope used in counting the grains was equipped with a "netzmikrometer" scale. Both the normal and the aborted grains falling within a certain area of the field marked out by the squares in the scale were counted. Two hundred or more grains were included in each count. Table VII gives the average results of five such counts made from as many different flowers taken from different parts of the same plant. A similar study was made with all available plants growing in the wild. Table VIII (p. 21) gives a summary of data obtained. The micro-photographs shown in plates V to XII, inclusive, show this

TABLE VII. SHOWING PERCENTAGE OF ABORTED GRAINS IN CERTAIN SPECIES OF RUBUS GROWING UNDER CULTIVATION

No.	Plant name	Percentage aborted grains
4-1	R. *allegheniensis* Porter	4.00
212-1	R. *allegheniensis* Porter	6.50
116-1	R. *flagellaris* Willd.	10.75
216-2	R. *baileyanus* Britton	11.05
137-4	R. *abbrevians* Blanchard	11.60
136-1	R. *frondisentis* Blanchard	12.15
8-2	R. *baileyanus* Britton	13.65
205-1	R. *permixtus* Blanchard	46.85
211-1	R. *plicatifolius* Blanchard	65.00
215-1	R. *plicatifolius* Blanchard	65.00
7-2	R. *allegheniensis* × *frondosus*	69.25
17-4	R. *frondosus* Bigelow	72.00
105-8	R. *groutianus* Blanchard	72.00
134-4	R. *groutianus* Blanchard	77.75
17-5	R. *frondosus* Bigelow	77.75
17-1	R. *frondosus* Bigelow	78.75
256-3	R. *elegantulus* Blanchard	78.75
220-3	R. *andrewsianus* Blanchard	81.75
34-1	R. *setosus* Bigelow	81.95
121-3	R. *brainerdi* Rydb.	82.75
121-1	R. *brainerdi* Rydb.	83.50
12-3	R. *vermontanus* Blanchard	84.80
12-4	R. *vermontanus* Blanchard	87.00
14-2	R. *jacens* Blanchard	88.14
13-2	R. *canadensis* L.	91.34
203-1	R. *hispidus* Bigelow	93.75
119-2	R. *setosus* Bigelow	94.50
13-1	R. *orarius* Blanchard	94.50

variation in the number of aborted grains in some of the species and hybrids studied. These micro-photographs not only show a large difference in the percentage of aborted pollen but also a difference in the size of the normal pollen grains (all the grains shown in these plates are 85 diameter magnifications). This difference in the size of the normal pollen grains is interesting in that there seems to exist a correlation between the size of the mature "seed" and the size of the pollen. The small-sized "seeds" and the small-sized pollen grains are characteristics of the high-bush blackberries of the

TABLE VIII. SHOWING PERCENTAGE OF ABORTED GRAINS IN CERTAIN SPECIES OF RUBUS COLLECTED IN THE WILD

Plant name	Percentage aborted grains
R. allegheniensis Porter	4.45
R. baileyanus Britton	9.84
R. frondisentis Blanchard	9.86
R. enslenii Tratt.	11.14
R. abbrevians Blanchard	12.46
R. flagellaris Willd.	12.81
R. invisus (Bailey) Britton	14.84
R. argutus L.	21.24
R. permixtus Blanchard	51.14
R. jeckylanus Blanchard	58.88
R. glandicaulis Blanchard	59.14
R. fraternis B. & P.	61.15
R. plicatifolius Blanchard	64.85
R. recurvans var. subrecurvans Blanchard	64.85
R. multispinus Blanchard	65.30
R. flavinanus Blanchard	66.90
R. baileyanus × *hispidus*	68.14
R. pergratus Blanchard	68.45
R. elegantulus Blanchard	68.94
R. allegheniensis × *frondosus*	69.25
R. allegheniensis × *pergratus*	74.12
R. canadensis × *elegantulus*	74.68
R. elongatus B. & P.	74.80
R. groutianus Blanchard	75.16
R. frondosus Bigelow	77.14
R. arenicola Blanchard	77.68
R. setosus Bigelow	79.81
R. andrewsianus Blanchard	81.04
R. junceus Blanchard	82.25
R. brainerdi Rydb.	83.15
R. jacens Blanchard	84.16
R. canadensis L.	84.64
R. elegantulus × *vermontanus*	86.04
R. vermontanus Blanchard	86.12
R. trifrons Blanchard	87.94
R. frondosus × *vermontanus*	88.24
R. canadensis × *pergratus*	89.42
R. semisetosus Blanchard	90.81
R. vermontanus var. viridifolius Blanchard	91.45
R. cubitans Blanchard	92.15
R. hispidus L.	92.45
R. orarius Blanchard	94.50

R. allegheniensis Porter type while the procumbent types are large "seeded" and have comparatively large pollen. This can be seen from table IX, which gives the average size of both "seed" and pollen grain of New England species.

TABLE IX. GIVING WEIGHT OF "SEEDS" AND DIAMETER OF POLLEN GRAINS OF NEW ENGLAND SPECIES OF RUBI

Name	Average weight of "seed" in mg.	Average diameter of pollen grain in microns
R. allegheniensis Porter	15.96	21.75
R. argutus Link	16.40	21.90
R. pergratus Blanchard	18.70	24.15
R. frondosus Bigelow	19.12	24.10
R. frondosus Bigelow, form *recurvans* Blanchard	19.10	24.30
R. canadensis L.	20.19	23.40
R. elegantulus Blanchard	20.15	24.75
R. vermontanus Blanchard	28.60	25.00
R. setosus Bigelow	31.40	28.75
R. hispidus L.	35.42	31.15
R. flagellaris Willd.	34.53	29.70
R. enslenii Tratt.	36.53	29.04
R. baileyanus Britton	38.60	30.65

The data presented in the three preceding tables may be summarized as follows:

1. The amount of aborted pollen in the different species varies from 4.00 percent in *R. allegheniensis* Porter to 94.5 percent in *R. setosus* Bigelow and *R. allegheniensis* × *canadensis*. The species showing the least amount of aborted pollen are either the extreme high-bush type like *R. allegheniensis* Porter or the extreme procumbent type like *R. flagellaris* Willd., *R. baileyanus* Britton and *R. enslenii* Tratt. The intermediate species and hybrids show a comparatively large amount of aborted pollen.

2. The size of the pollen grains as well as the size of the "seed" show this same general variation. The high-bush types of blackberry have comparatively small pollen grains and small "seeds," while in the procumbent blackberries the reverse is true.

STERILITY AS SHOWN BY POLLEN GERMINATION

The mature pollen grain may in some instances be perfectly normal both in appearance and size and yet not be functional. Dorsey (19), working with the grapes and Geertz (25) working with the evening primroses, found this to be of common occurrence. Sandsten (17), Martin (23), and others (22), working on the physiology of the pollen of various fruits and agricultural plants, compute the amount of sterility in a given species by the percent of grains capable of germinating in a certain medium. The results thus obtained would be based upon the amount of apparently functional pollen. However, the variation shown in the germinating power of the same pollen in different media and under different light and temperature conditions makes this method unreliable except for comparative studies. Adams (22) found in working with the pollen of the apple and other members of the Rosaceæ family that a temperature of 21° to 23° C. gave the quickest germination and that the best germination was obtained in a cane sugar solution of varying percentage, depending upon the species used. He gives the following as the optimum concentration for pollen germination in the plants named: Apple 2.5-10 percent, pear 4-8 percent, strawberry 8 percent, loganberry 4 percent, raspberry 16 percent, black currant 16 percent. Sandsten (17) in an earlier work obtains somewhat similar results. He also showed that light affects the direction of growth of the pollen tube.

In order to check the reliability of aborted pollen as an index of sterility a comparative study was made of pollen germination in all plants listed in table VII (p. 20). Pollen from newly dehisced anthers were used. Various nutrient media were tried, including glycerin, olive oil, glucose, stigma and style decoctions, etc., but a 12 percent cane sugar solution gave the best results and this medium and concentration were used in all later germination tests. In sugar solutions of 9 percent or less concentration the pollen tubes would grow to a certain length and then burst, while in a solution of greater concentration than 12 percent the growth was retarded or completely checked. The optimum temperature for the germination of the pollen was found to be 22° C. The pollen was mounted in ordinary hanging drop culture slides similar to the ones used by Sandsten (17), but an opening was left between the slide and the cover-glass so as to admit the air from the outside. These were then placed in a dark, moist air germinator gauged at a temperature of 22° C. and left to germinate for 24 hours when the final count was made. Table X gives the average results of counts made from four such mounts of pollen taken from at least four different flowers on the same plant. Plates XIII to XVI, inclusive, are micro-photographs of some of these mounts, showing the difference in germination.

By a comparison of the percentage germination and the percentage of aborted pollen in the given species (tables VII and X, pp. 20 and 24) it will be seen that in some plants (like *R. allegheniensis* × *frondosus*) a large number of grains failed to develop pollen tubes. This would indicate a relatively large amount of normal-sized, sterile pollen, while in species like *R. allegheniensis* Porter little or no morphologically perfect pollen is functionless.

TABLE X. SHOWING PERCENTAGE OF POLLEN GERMINATION

No.	Plant name	Percentage of pollen germinating
121-1	*R. brainerdi* Rydb.	1.00
203-1	*R. hispidus* L.	1.00
119-2	*R. setosus* Bigelow	1.00
121-3	*R. brainerdi* Rydb.	1.10
34-1	*R. setosus* Bigelow	1.18
220-3	*R. andrewsianus* Blanchard	1.20
215-1	*R. plicatifolius* Blanchard	1.25
13-1	*R. orarius* Blanchard	1.52
13-2	*R. canadensis* L.	2.72
12-4	*R. vermontanus* Blanchard	2.75
12-3	*R. vermontanus* Blanchard	2.80
134-4	*R. groutianus* Blanchard	3.95
256-3	*R. elegantulus* Blanchard	4.20
14-2	*R. jacens* Blanchard	4.28
105-8	*R. groutianus* Blanchard	4.30
17-4	*R. frondosus* Bigelow	4.40
17-5	*R. frondosus* Bigelow	4.52
17-1	*R. frondosus* Bigelow	4.55
7-2	*R. allegheniensis* × *frondosus*	5.00
211-1	*R. plicatifolius* Blanchard	6.75
136-1	*R. frondisentis* Blanchard	39.94
137-4	*R. abbrevians* Blanchard	46.12
205-1	*R. permixtus* Blanchard	53.00
216-2	*R. baileyanus* Britton	59.33
8-2	*R. baileyanus* Britton	64.24
116-1	*R. flagellaris* Willd.	82.00
212-1	*R. allegheniensis* Porter	93.50
4-1	*R. allegheniensis* Porter	94.50

A great difference in the rapidity of growth of the pollen tubes was noted for the different species (table XI, p. 25). It was found by a series of repeated tests that the growth of the pollen tube was quite constant for a given species, but varied greatly for the different species or forms. Table XI (p. 25) shows the rapidity of growth of the pollen tubes of some of the common forms of blackberries. These pollen grains were germinated in a 12 percent cane sugar solution as previously described. The length given in every instance is the average of 12 measurements from four such mounts. The measurements for the length of the pollen tube are quite reliable for the first eight hours of the germination period, since the cultures were almost free from bacterial growth during that time. After being in the germinator for 12 hours the cultures were as a rule affected by the growth of fungi or bacteria, which would necessarily make the measurements then obtained more unreliable.

TABLE XI. SHOWING THE DIFFERENCE IN THE RATE OF GROWTH OF THE POLLEN TUBES

	Average length of pollen tubes in microns after germinating in a 12 percent sugar solution for						
Name	**½ hr.**	**1 hr.**	**2 hrs.**	**3 hrs.**	**4 hrs.**	**8 hrs.**	**24 hrs.**
R. *baileyanus* Britton	16	32	190	312	558	1146	1377
R. *permixtus* Blanchard	24	44	146	280	449	711	848
R. *enslenii* Tratt.	18	30	138	308	510	1016	1248
R *allegheniensis* Porter	16	42	140	218	332	480	746
R. *abbrevians* Blanchard	14	35	120	198	304	468	704
R. *frondosus* Blanchard	4	21	93	182	276	475	725
R. *flavinanus* Blanchard	5	24	59	83	158	316	498
R. *brainerdi* Rydb.	5	26	55	79	125	293	466
R. *andrewsianus* Blanchard	0	1	32	94	103	231	449
R. *pergratus* Blanchard	2	12	18	35	70	180	416
R. *vermontanus* Blanchard	1	11	16	32	64	173	400
R. *setosus* Bigelow	11	16	48	73	92	177	325
R. *canadensis* L.	0	0	29	88	156	316	347
R. *hispidus* L.	0	0	16	32	108	204	278
R. *trifrons* Blanchard	0	0	12	20	32	100	244

An attempt was made to determine the comparative rapidity of growth of the pollen tube as it penetrates the style. Several flowers of *R. vermontanus* Blanchard were emasculated and bagged in the usual manner. Two days later one-half of these emasculated flowers were pollinated with the pollen from *R. permixtus* Blanchard, while the other half were pollinated with the pollen from another plant of *R. vermontanus* Blanchard. A number of these flowers were then "fixed" in a chromo-acetic acid killing solution, 12, 24 and 30 hours after pollination had been effected. Later, cytological studies of these flowers showed that fertilization took place at least six hours earlier in the flowers which had been pollinated with pollen from *R. permixtus* Blanchard than in the flowers which had been close-pollinated.

If there is such a difference in the rate of growth of the pollen tubes as shown in the preceding data, then in the wild, where insect cross-pollination is the rule, it becomes a very important factor in reference to spontaneous hybridization. This difference in the rate of growth of the pollen tube may account for the very frequent occurrence of certain natural hybrids and the less frequent occurrence or entire absence of other hybrid forms although the two parent species may be growing side by side.

STERILITY AS SHOWN BY HYBRIDIZATION

If spontaneous hybridization takes place among the different species of wild blackberries, as would seem highly probable from the data obtained in the preceding studies, it should be possible to produce similar hybrids by artificial cross-fertilization.

The difficulty of selecting the elementary species from among the now existing numerous forms by the ordinary taxonomic means becomes obvious. After a thorough systematic study of the group, however, certain plants were selected which showed marked specific differences and which were suspected of interbreeding. These in particular were used in hybridization work.

The plants were grown in a cage covered with ordinary galvanized mosquito netting (plate XVII) which not only protected the bags and plants from insect injury, but also from being tampered with by intruders. All cross-fertilization work, which was done by the usual bagging method, was carried on inside this cage.

In order to determine the earliest time at which self-pollination might occur, a series of checks were used similar to those used by Wellington (26) in working with the raspberries. Flowers in different stages of development were emasculated and bagged in the usual manner. These were then left without being pollinated. Table XII (p. 27) shows in detail the number of flowers of the species and hybrids used and their stages of development when emasculated. The lower number represents the number of flowers emasculated, while the upper represents the number of seeds formed. In no instances were there any seeds formed where emasculation had been affected prior to the time when the corolla opened and there were but four seeds formed from the entire series of checks. Cytological examination of the flowers also revealed the fact that the pollen sacs do not split open until after the corolla has unfolded. For the sake of precaution, however, all flowers used in the hybridization work were emasculated before the splitting of the calyx took place. Checks were also used in most cases.

The crosses affected during the seasons 1914, 1915 and 1916 are summarized in table XIII (p. 28). The lower number represents the number of flowers cross-pollinated, while the upper represents the number of seeds formed. It will be noted that in nearly all flowers cross-pollinated where "good" pollen was used a large percent of ovules formed seeds. Flowers pollinated with pollen

TABLE XII. SHOWING CHECKS USED IN CROSS-FERTILIZATION WORK

The lower number represents the number of flowers emasculated and the upper number represents the number of seeds formed.

	Very young flowers	About two days before calyx split	About one day before calyx split	Calyx beginning to split	Corolla just showing	Corolla quite conspicuous	Just before corolla unfolds	Just after corolla has unfolded
R. canadensis L.	0 3	0 6	0 6	0 11	0 2	0 8	0 4	0 6
R. allegheniensis Porter	0 4	0 2	0 7	0 12	0 8	0 14	0 3	0 8
R. vermontanus Blanchard	0 2	0 11	0 14	0 3	0 7	0 7	0 6	0 12
R. frondosus Bigelow	0 1	0 6	0 11	0 3	0 4	0 6	0 8	4 14
R. allegheniensis × *frondosus*		0 3	0 5	0 4	0 5	0 4	0 1	0 13

from plants such as *R. allegheniensis* Porter or *R. baileyanus* Britton gave a greater percent of mature seeds than if these same plants had been close-pollinated (see table VI, p. 18). On the other hand, whenever a form having a large amount of aborted pollen was used as the male parent comparatively few ovules developed seeds. It will also be noted that none of the attempted crossings failed to produce viable seeds where a reasonable number of flowers were used. The few flowers in which no seed were developed may have been somewhat injured during the process of emasculation or pollination may not have been affected at the proper time.

TABLE XIII. SHOWING CROSSES MADE DURING 1914, 1915 AND 1916. THE LOWER NUMBER REPRESENTS THE NUMBER OF FLOWERS CROSS-POLLINATED WHILE THE UPPER NUMBER REPRESENTS THE NUMBER OF SEEDS FORMED

	R. allegheniensis Porter ♀	*R. andrewsianus* Blanchard ♀	*R. permixtus* Blanchard ♀	*R. allegheniensis* × *frondosus* ♀	*R. orarius* Blanchard ♀	*R. frondosus* Blanchard ♀	*R. canadensis* L. ♀	*R. vermontanus* Blanchard ♀	*R. setosus* Bigelow ♀	*R. baileyanus* Britton ♀	*R. jacens* Blanchard ♀
R. allegheniensis		170		230	1024	157	143	147	124		
Porter ♂		7		9	35	14	7	4	9		
R. andrewsianus						2					
Blanchard ♂						2					
R. permixtus						28					
Blanchard ♂						3					
R. allegheniensis ×	290			2		11	4				
frondosus ♂	9			3		1	1				
R. orarius	70										
Blanchard ♂	12										
R. frondosus	60	2			21		14	3		11	
Blanchard ♂	3	1			11		3	1		1	
R. canadensis L. ♂	22				8	2					
	3				4	5					
R. vermontanus	3				22	22	3				5
Blanchard ♂	1				10	2	2				4
R. setosus	2						14				
Bigelow ♂	1						8				
R. baileyanus						0	18				
Britton ♂						1	3				
R. jacens							34	38			23
Blanchard ♂							8	4			5
Average number of ovules per flower	84	72	29	66	77	72	68	42	38	46	23

The above data would indicate:

1. That sterility among the blackberries is largely due to defective pollen.

2. That all blackberries are capable of inter-breeding under favorable conditions for doing so, since some of the crosses effected were between plants as remotely related as *any* two species of Eubatus.

THE FIRST GENERATION OF ARTIFICIAL HYBRIDS

The seeds produced by the hybridization work as outlined in table XIII were collected (the original bags having been left enclosing the flower until the drupelets had fully matured) and planted in sand in the ordinary greenhouse flats. It was found that if the fruit were left in a glass tumbler to ferment for a few hours, the pulp could more easily be removed. All sand used for planting was thoroughly heated in a dry oven in order to kill any seeds that might be present as it was found that nearly all New England surface soil contains blackberry and raspberry seeds in quite large numbers. These have undoubtedly been carried by birds. The flats were then placed outdoors in a cage where they were also protected by a layer of cloth. It was found that some of the seed of the dewberry types would germinate the following spring, but most of the high-bush forms require two years for germination. Table XIV shows the number of seedlings obtained from these plantings. Some of these were winter-killed during the first year, but at present there are representatives of most of these hybrids growing in the Vermont Station gardens. All of these plants show a more or less degree of intermediacy between the two parent forms not only in respect to the shape of leaf and the character and abundance of simple hairs, gland-tipped hairs and prickles, but also in respect to the type of flower and fruit in those cases where the plants are mature enough to form these structures. For example, the 10 plants obtained from the cross effected in the spring of 1914 between No. 4-1, *R. allegheniensis* Porter as the pistillate plant and No. 17-3, *R. frondosus* Bigelow as the staminate

TABLE XIV. SHOWING NUMBER OF HYBRID PLANTS GROWN FROM SEED PRODUCED BY ARTIFICIALLY FERTILIZED FLOWERS

Parent plants	Number of seedlings grown
**R. allegheniensis* Porter × *R. allegheniensis* × *frondosus*	78
R. allegheniensis Porter × *R. andrewsianus* Blanchard	10
**R. allegheniensis* Porter × *R. canadensis* L.	101
**R. allegheniensis* Porter × *R. frondosus* Bigelow	52
**R. allegheniensis* Porter × *R. orarius* Blanchard	121
**R. allegheniensis* Porter × *R. setosus* Bigelow	110
**R. allegheniensis* Porter × *R. vermontanus* Blanchard	41
R. allegheniensis × *frondosus* × *R. canadensis* L.	3
R. allegheniensis × *frondosus* × *R. frondosus* Bigelow	4
**R. andrewsianus* Blanchard × *R. frondosus* Bigelow	1
R. baileyanus Britton × *R. canadensis* L.	6
R. baileyanus Britton × *R. frondosus* Bigelow	8
**R. canadensis* L. × *R. frondosus* Bigelow	11
R. canadensis L. × *R. jacens* Blanchard	12
R. canadensis L. × *R. orarius* Blanchard	1
R. canadensis L. × *R. setosus* Bigelow	3
R. frondosus Bigelow × *R. orarius* Blanchard	7
R. frondosus Bigelow × *R. permixtus* Blanchard	12
R. frondosus Bigelow × *R. vermontanus* Blanchard	16
**R. jacens* Blanchard × *R. vermontanus* Blanchard	23
R. orarius Blanchard × *R. vermontanus* Blanchard	3

---

*Reciprocal crosses are included in this number.

plant are almost duplicates of No. 7-1, which was found growing four miles north of Burlington and which is a suspected wild hybrid between *R. allegheniensis* Porter and *R. frondosus* Bigelow. The same is true in general of the other hybrid plants produced artificially, their duplicate have in most cases been found growing in the wild.

SEGREGATION IN NATURAL HYBRIDS

Seedlings were grown from the selfed flowers of nearly all the wild forms of blackberries grown in the Vermont Station gardens. The seeds from which these plants were grown were treated in the same manner as those germinated in the hybridization work which has already been discussed. Many of these plantings show very clearly a more or less complete reversion towards two or more of the stable forms of blackberries. None of the first generation plants showed any well-defined Mendelian segregation. There always occur a large number of variants between the two extreme forms and the differences between the individual plants of any given progeny were so slight that no definite class-groups could be made. The data obtained from these sowings are summarized in table XV. The terms "extremely

TABLE XV. GIVING A SUMMARY OF THE VARIATION FOUND IN THE PROGENY OF SELFED PLANTS

Name of plant	Degree of variation
R. abbrevians Blanchard	Somewhat variable
R. allegheniensis Porter	Not variable
R. allegheniensis × *frondosus*	Very variable
R. andrewsianus Blanchard	Very variable
R. arenicola Blanchard	Somewhat variable
R. baileyanus Britton	Not variable
R. baileyanus × *hispidus*	Very variable
R. brainerdi Rydb.	Somewhat variable
R. canadensis L.	Not variable
R. cubitans Blanchard	Very variable
R. elegantulus Blanchard	Not variable
R. flagellaris Willd.	Not variable
R. falvinanus Blanchard	Very variable
R. frondisentis Blanchard	Not variable
R. frondosus Bigelow	Somewhat variable
R. groutianus Blanchard	Very variable
R. hispidus L.	Not variable
R. jacens Blanchard	Extremely variable
R. junceus Blanchard	Very variable
R. orarius Blanchard	Very variable
R. pergratus Blanchard	Not variable
R. permixtus Blanchard	Somewhat variable
R. recuvicaulis Blanchard	Variable
R. setosus Bigelow	Not variable
R. trifrons Blanchard	Extremely variable
R. vermontanus Blanchard	Not variable

variable," "very variable," "variable," "somewhat variable," and "not variable" are used to designate in a general way the degree of variation found within a given progeny. Several individual sowings with the seeds of plants taken from different stations are represented in each of the bi-nomials given in this table. Plates XVIII. and XIX. are photographs of several seedlings showing segregation.

Such segregation as noted above can only occur in plants of hybrid origin. The following natural hybrids show a definite segregation towards the species given opposite them and may, therefore, be assumed to have been produced by these species hybridizing in the wild:

R. *allegheniensis* × *frondosus*	R. *allegheniensis* × *frondosus*
R. *andrewsianus* Blanchard	R. *allegheniensis* × *argutus*
R. *arenicola* Blanchard	R. *baileyanus* × *frondosus*
R. *baileyanus* × *hispidus*	R. *baileyanus* × R. *hispidus*
R. *cubitans* Blanchard	R. *hispidus* × *vermontanus*
R. *flavinanus* Blanchard	R. *allegheniensis* × *elegantulus*
R. *groutianus* Blanchard	R. *elegantulus* × *setosus*
R. *jacens* Blanchard	R. *hispidus* × *setosus*
R. *junceus* Blanchard	R. *canadensis* × *setosus*
R. *orarius* Blanchard	R. *allegheniensis* × *canadensis*
R. *permixtus* Blanchard	R. *allegheniensis* × *hispidus*
R. *trifrons* Blanchard	R. *hispidus* × *setosus*

Based upon other hybrid characters aside from segregation in the offspring, other so-called species have been assumed to be spontaneous hybrids. These have already been treated in a recent bulletin from this Station (1).

GENERAL DISCUSSION OF THE RESULTS OF THE EXPERIMENT

It has been shown that inter-breeding among the many different species of blackberries is easily effected. It would, therefore, seem highly probable that such inter-breeding occurs spontaneously in a group like this where insect cross-pollination is the rule. That such inter-breeding does occur seems evident from the variability which characterizes the entire group. That the individual forms within this group should be so variable and that all so-called species of blackberries should have certain marked characters in common, seems to indicate their common origin through hybridization. Moreover, the progeny of a large number of these so-called species shows segregation towards the more stable forms which is an unmistakable character of hybrids.

The pronounced difference in the amount of sterility and other hybrid characters in the different species seems to indicate that all the present New England forms have been brought about by the interbreeding of two or more elementary species. These are now represented by the extreme high-bush type as *R. allegheniensis* Porter and the extreme procumbent type as *R. baileyanus* Britton or *R. enslenii* Tratt. If such is the case, the several intermediate stable forms, such as *R. setosus* Bigelow, *R. vermontanus* Blanchard, etc., are simply remotely or recently formed cryptohybrids. This would account for the great amount of sterility found in these species.

SUMMARY

1. Variations due to external factors are very marked in the plants of the Eubatus group. This is especially true in reference to protodermal outgrowths. Their development depends largely upon external factors and they are, therefore, of little taxonomic value.
2. Light seems to be the determining factor affecting the development of protodermal outgrowths.
3. The primordia of the prickle, glandular hair, and simple hair are present in all species of blackberries. The prickle and glandular hair are morphologically simple and the former may develop from the latter.
4. A large percentage of infertility occurs in most species of blackberries. This is shown not only by the large amount of aborted pollen present in most species, but also by bagging, pollen germination, and hybridization experiments.
5. Sterility among the blackberries is largely due to defective pollen.
6. The percentage of infertility in a given species is quite constant. This has been shown by several methods.
7. The two extreme types of blackberries, *R. allegheniensis* Porter and *R. baileyanus* Britton, show less infertility and other hybrid characters than any of the intermediate species or forms.
8. These two types possess certain well-marked quantitative characters, such as size of seed, size of pollen grain, etc., which are present in compromise form in all the intermediate species and forms.
9. Cross-pollination is the rule in all species of blackberries. All species of Rubus studied are either nearly or completely self-sterile.

10. All New England blackberries are capable of inter-crossing under favorable conditions for doing so.

11. Duplicates of natural hybrids have been produced by artificial hybridization.

12. The progeny of a number of so-called species of blackberries segregate, a character which is present only in organisms of hybrid origin.

13. In view of the data presented, it is concluded that spontaneous hybridization is quite common in the Eubatus group and that a large number of the so-called species are either hybrids or cryptohybrids brought about probably by the inter-breeding of two or more elementary species.

LITERATURE CITED

(1) BRAINERD, EZRA, and PEITERSEN, A. K. Blackberries of New England—Their Classification. Vt. Sta., Bul. 217. (1920.)

(2) BICKNELL, E. P. Have We Enough New England Blackberries? Bul. Torrey Club, Vol. 37, p. 393. (1910.)

(3) LOTHELIER, M. A. Recherches sur les Plantes a Piquants. Rev. Gen. Bot., Vol. 5, pp. 480-483, 518-528. (1893.)

(4) ZEIDIER, VON J. Uber den Einfluss der Luftfeuchtigkeit und des Lichtes auf die Ausbildung der Dornen von Ulex europaeus L. Flora. Vol. 102, pp. 87-95. (1911.)

(5) COULTER, J. M., BARNES, C. E., and COWLES, H. C. A Text-book of Botany, Vol. 2, pp. 741-744. Chicago. (1911.)

(6) JEFFREY, E. C. Some Fundamental Morphological Objections to the Mutation Theory of DeVries. Amer. Nat., Vol. 49, pp. 5-21. (1915.)

(7) GAERTNER, C. F. Versuche und Beobachtungen über die Bastardezeugung im Pflanzenreich. Stuttgart. (1849.)

(8) GRIEVE, P. The Sterilty of Hybrids. Garden, Vol. 10, pp. 67, 150. (1876.)

(9) WILSON, J. H. Infertile Hybrids. Rept. Internat. Conf. on Genetics. Vol. 3, pp. 183-209, figs. 32-49. (1906.)

(10) ROSEN, F. Die Entstehung elementarer Arteen aus Hybridtion ohne Mendelsche Spaltung. Beitr. Pflanzenzucht, Vol. 3, pp. 89-99. (1913.)

(11) BATESON, W. Problems of Genetics. New Haven. (1913.)

(12) JEFFREY, E. C. The Mutation Myth. Science, N. S., Vol. 39, pp. 488-491. (1914.)

(13) JEFFREY, E. C. Spore Conditions in Hybrids and the Mutation Hypothesis of DeVries. Bot. Gaz., Vol. 58, pp. 322-336. (1914.)

(14) JEFFREY, E. C. Hybridism and the Rate of Evolution in Angiosperms. Amer. Nat., Vol. 50, 129-143. (1916.)

(15) HOLDEN, R. Hybrids of the Genus Epilobium. Amer. Nat., Vol. 50, 243-247. (1916.)

(16) HOAR, C. S. Sterility as the Result of Hybridization and the Condition of Pollen in Rubus. Bot. Gaz., Vol. 62, pp. 370-388. (1916.)

(17) SANDSTEN, E. P. Some Conditions Which Influence the Germination and Fertility of Pollen. Wis. Sta., Rsch. Bul. 4. (1909.)

(18) BAILEY, L. H. The Evolution of Our Native Fruits. New York. (1898.)

(19) DORSEY, M. J. Pollen Development in the Grape with Special Reference to Sterility. Minn. Sta., Bul. 144. (1914.)

(20) LUTZ, A. M. A Study of the Chromosomes of Oenothera Lamarckiana, Its Mutants and Hybrids. Proc. Internat. Zool. Congress. Boston. pp. 352-354. (1907.)

(21) FOCKE, W. O. Synopsis Ruborum Germaniae. (Bremen.) (1877.)

(22) ADAMS, J. On the Germination of the Pollen Grains of Apple and Other Fruit Trees. Bot. Gaz., Vol. 61, pp. 131-147. (1916.)

(23) MARTIN, J. N. The Physiology of the Pollen of Trifolium Pratense. Bot. Gaz., Vol. 56, 112-126. (1913.)

(24) WESTGATE, J. M., and others. Red-clover Seed Production; Pollination Studies. U. S. Dept. Agr., Bu. Pl. Ind., Bul. 289. (1915.)

(25) GEERTZ, J. M. Cytlolgische Untersuchungen einiger Bastarde von Oenothera gigas. Ber. Deutsch. Bot. Gesells., Vol. 29, pp. 160-166. (1911.)

(26) WELLINGTON, R. Raspberry Breeding. Proc. Soc. Hort. Sci., Vol. 10, pp. 155-159. (1913.)